JOURNAL

of the

LEPIDOPTERISTS' SOCIETY

THE LEPIDOPTERISTS' SOCIETY

EXECUTIVE COUNCIL

The object of the Lepidopterists' Society, which was formed in May, 1947 and formally constituted in December, 1950, is "to promote the science of lepidopterology in all its branches, ... to issue a periodical and other publications on Lepidoptera, to facilitate the exchange of specimens and ideas by both the professional worker and the amateur in the field; to secure cooperation in all measures" directed towards these aims.

Membership in the Society is open to all persons interested in the study of Lepidoptera. All members receive the *Journal* and the *News of the Lepidopterists' Society*. Institutions may subscribe to the *Journal* but may not become members. Prospective members should send to the Treasurer full dues for the current year, together with their full name, address, and special lepidopterological interests. In alternate years a list of members of the Society is issued, with addresses and special interests. There are four numbers in each volume of the *Journal*, scheduled for February, May, August and November, and six numbers of the *News* each year.

Cover illustration: First stage larva of *Natada nasoni* (Grote) (Limacodidae), from Dyar 1899, J. New York Entomol. Soc. 7:61–67. Suggested by Marc E. Epstein.

PRESIDENTIAL ADDRESS, 1984:
A TRIBUTE TO THE AMATEUR

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First of all, let me state that it has been a great pleasure to serve the Society as its president during the past year. This is a wonderful group and one of the few in this country where the professional and the amateur can speak as equals. But, all too often the statement is made: "He is only an amateur," usually implying that he doesn't know what he is talking about, or at least that his opinion is not worth as much as one who makes his living in the field. I do not accept this view, and this presentation is an unabashed tribute to those who do not make their living in the field of lepidopterology.

What is an amateur? The word is derived from the Latin *"amator"* (lover) or the French *"amare"* (to love), and is defined in the dictionary as "one who cultivates a particular pursuit, study or science from taste, without pursuing it professionally." Everyone makes his or her living at something, and I consider an amateur lepidopterist as one who makes his living at something other than lepidopterology. There can, then, be janitors, pipefitters, medical doctors, engineers and mammalian ecologists using lepidopterology as an avocation. There are good amateur workers in the field and bad ones, but the variant definition of amateur is not always applicable: "one practicing an art without mastery of its essentials." I am praising that amateur who has gained a certain amount (often a great deal) of expertise in a particular phase of lepidopterology, enough so that he or she is able to impart that knowledge to others.

Amateurs have been the backbone of science since its inception: there were no professional entomologists in Linnaeus' time, but no one suggests that they did not do the best possible job with the information

available to them. Pieter Cramer was an artist whose avocation was lepidopterology; Dru Drury was a silversmith; Jacob Huebner was a printer; William Chapman Hewitson was a wealthy landowner and otherwise retired; William Henry Edwards was a coal baron; Henry Edwards was an actor; William Barnes was a physician, and Walter Rothschild was a "black sheep" who did not fit into the family banking business. From these diverse backgrounds, however, came people who made tremendous contributions to the field of lepidopterology, as great as those of the contemporaneous professionals. Most of the contributions that have been made by amateurs have been in systematics, behavior, life history, morphology and ecology, subsets of the field that usually require less elaborate equipment; but a number of important contributions also have been made in the field of genetics by non-professionals.

Often the amateur will attack a problem of limited scope and become very expert on that topic. The amateur may be expected to gather much pertinent material within a circumscribed group, often more and better material than is readily available to the professional even in the finest of facilities. He studies the material gathered, including that which is borrowed from museum collections, and gathers together the appropriate literature, just as the professional would. He is at least as likely as the professional to ask opinions from others, and most studies done by amateurs go through a great many more drafts, and hands for comment, than do papers written by those of us in the profession for the simple reason that the amateur is still convinced that he does not know everything there is to know. Most publishing amateurs are at least as receptive to new and different ideas as are those of us who do it for a living.

Admittedly, I am talking here of the *best* amateurs, not those unguidable persons who nevertheless write on various subjects without the benefit of knowledge or guidance. The "good" amateurs are the ones who behave in the field about as we should expect professionals to perform their studies.

The early amateurs worked chiefly in systematics of Lepidoptera. They generally amassed huge (for the day), usually beautifully curated collections of specimens, and spent much of their time writing descriptions of new taxa from these collections or from those of their acquaintances. Certainly this is what W. C. Hewitson, W. H. Edwards and Henry Edwards, to name a few, did, and their works compare favorably to those of Butler, Walker and other professionals of the day. Once in a while one hears grumblings about the incompleteness by today's standards of their descriptions, but one also hears this complaint about the descriptions done by professionals of the same time period.

Later, other amateurs like Frederick DuCane Godman and Osbert Salvin, two wealthy English "men of leisure", began looking at Lepidoptera as related populations of organisms, rather than as specimens which either varied from other specimens or did not. These amateurs began putting contemporary biological theories into practice and critically examined lepidopteran populations in light of the then new ideas of evolution and biogeography. The result was that they, mostly with Godman's money, decided to do a total biological inventory of Mexico and Central America for which they would write some parts and enlist experts in other fields to contribute sections. The resulting *Biologia Centrali-Americana* was published over more than 30 years and ran to nearly fifty sumptuous volumes. This publication still has not been superceded.

Walter Rothschild, once he decided to collect Lepidoptera seriously, could have been expected to do it with a vengeance. He did, finally amassing something over two and a quarter million specimens, more than the Lepidoptera holdings of most of today's major museums. He immediately saw the advantages of collecting study series, and for the first time, a private collection had more than a few specimens of any single taxon. At the same time in France, a printer, Charles Oberthuer, began much the same type of accumulation of material, although the scope of his collecting was smaller than Rothschild's. Oberthuer's collection finally amounted to more than a million specimens. Rothschild was one of the first private collectors to realize that he probably needed professional curatorial help, and he hired Karl Jordan as entomologist at his museum and Ernst Hartert as his ornithological curator. What a team they made! If one goes through the writings of this triumvirate, one can find the first modern concept of geographical subspecies, trinominal nomenclature, an elucidation of the biological species concept, and one of the first cladistic analyses of an animal group (it was not so labelled and frequently is not recognized as such). Especially with Walter Rothschild and his curators, modern systematics can be shown to have had its birth. To say that I am a Rothschild fan would be true because of the facts that he (A) collected long series of material for study, (B) had a worldwide bias to his activities, and (C) surrounded himself with those who in conjunction with him developed most of the bases of modern systematics. Their efforts were not always appreciated by their contemporaries, but those must have been halcyon days at Tring!

Strangely enough, another man lived in England at the same time who had an obsession with outdoing Rothschild, thereby setting himself a prodigious task. James J. Joicey was a man of leisure who decided that he would outdo Rothschild in the acquisition of orchids. He tried

this for some years before and during World War I, finally going bankrupt for 30,000 pounds, a very large sum at the time. The judge admonished Joicey, and he agreed that he would not try to build the world's premier orchid collection, and he held to his promise. He switched instead to Lepidoptera and went broke in the 1930's for over 300,000 pounds, perhaps making a statement about how deeply one can get involved in making a collection if one lets his or her imagination run wild. Joicey did, however, hire curators (perhaps because Rothschild had them), and they produced some excellent work, especially on the Lepidoptera of New Guinea, Hainan Island, and central and eastern Africa. The Joicey, Oberthuer and Rothschild collections are the reason that the British Museum (Natural History) enjoys such numerical superiority over other collections throughout the world.

In the United States, Dr. William Barnes, a physician from Decatur, Illinois, formed a magnificent collection of North American Lepidoptera. It became readily apparent that many specimens that he was obtaining were undescribed, and with the help of professional curators, he set about to describe them. From this activity came revisionary studies on moth genera which are still standard today. Many of these were published in his own journal, *Contributions to the natural history of the Lepidoptera of North America,* and were often jointly coauthored with his curators, Arthur Ward Lindsey, James McDunnough, and Foster H. Benjamin, among others. Many of the finest contributions during the first quarter of the 20th Century came from that journal.

In later years, many amateurs have made contributions to the taxonomy of Lepidoptera. Without exception, these students have been willing to listen to others and be guided by them, and the resulting papers have been highly informative. Anyone who has ever studied Hesperiidae knows of the legacy left us by Brigadier William Harry Evans, a retired British army officer who served in India during the first third of this century. His *Catalogues* to the hesperiids are standard works for the professional and the amateur alike. Many people forget that he also wrote the definitive guide to the butterflies of India, which is still being reprinted. Still, he was an amateur who performed like a professional. Another military man turned lepidopterist is John N. Eliot, recently awarded the Karl Jordan Medal, whose studies of the Lycaenidae and the *Neptis* group of nymphalids have earned him a permanent place in our field. He also completely revised Corbet and Pendlebury's *Butterflies of the Malay Peninsula.* Our former President, Col. Stanley S. Nicolay, has done some fine work tying together certain of the neotropical hairstreaks, and he is still trying to bring some order out of the chaos that characterizes this group. Stan also works on the hes-

periids, so it might be said that he has selected some very knotty problems to tackle. Surely the taxonomy of North American moths is better because of the activities of Mr. André Blanchard, a retired engineer. I have the utmost admiration for one who can tackle these little creatures and make sense of them. The late M. Henri Stempffer was a retired French banker who has added greatly to our knowledge of the taxonomy of African Lycaenidae, a group that has puzzled all workers before him. For his contributions M. Stempffer was elected to receive the first Jordan Medal given by this Society. We can expect other amateurs to receive the award in the future, I am sure. Arthur Rydon studied the Charaxini and has increased our knowledge of this group through his writings. Similarly, the recently deceased Dr. Lionel G. Higgins, an English physician, made a lifetime study of the Melitaeinae, and his writings are the basis of the classification of this group throughout the world. Our own former President and Honorary Life Member, Dr. F. M. Brown, is a geologist by trade, but he has achieved renown in the taxonomy of both nearctic and neotropical Rhopalocera, and if this is not enough, Brownie has now engaged (at more than 80 years old) in the study of fossil insects, and is writing several compendia on important groups. Cliff Ferris, another amateur subsequently elected President of our Society, is a bioengineer by profession, but his studies on the systematics of Nearctic butterflies are quite professional. Let us not forget the contributions of a former lawyer, Dr. Cyril F. dos Passos, who has worked for several decades on the taxonomy and nomenclature of North American butterflies. The list of amateurs who have contributed to the taxonomy of Lepidoptera is endless, and I apologize to others that I have left out—there simply is not enough space.

A special place must be saved for the late Dick Dominick whose dream of *The Moths of North America* has been an inspiration to us all. The several volumes that have appeared under the aegis of this series conspire to make the study of moths as popular as that of butterflies. It was an impressive project, and one can but wish that Dick had lived to see more of it completed.

To finally get to nontaxonomic studies, the life history studies done by Roy and Connie Kendall, their associates, and by those such as Dave Baggett have added the biological information that can turn alpha taxonomic treatises into studies at a higher level. They are providing the building blocks for greater understanding of Lepidoptera, and these studies cannot help but improve the quality of later studies on these insects. Amateur life history work generally does not include the chaetotaxy of the larvae that professionals consider vital, but the workers mentioned here are also preserving egg, larval, and pupal material for

such studies, and this material is readily available to those interested in performing them.

Dr. David Wright is a physician by occupation, still he is embarking on some superb micromorphological studies of various stages of butterflies, especially the Lycaenidae, using scanning electron microscopy, and he has already published new and innovative ideas on the morphology of the larval stages, including showing that some setae have wrongly been attributed to some segments when they belong to adjacent ones. To the casual observer, these data may seem trivial, but he has found at least one derived (apomorphic) character which seems to define the Lycaeninae, one that was previously unsuspected.

There are other examples of amateurs making contributions in ecology, physiology, and even genetics of Lepidoptera. The information that these workers are providing surely aids in the understanding of these insects. An example of such a study is Mike Fisher's rearing of *Papilio nitra* which unexpectedly turned up the fact that *Papilio zelicaon gothica* is the more frequent color morph of *nitra*. This was an elegant study, done on a low budget, that showed something totally unexpected.

My wife and I have been fortunate enough to work for and with a man with vision much like that of Rothschild. The late Arthur Allyn was the heart of an effort to form a real resource for taxonomic and morphological research on Macrolepidoptera. In the years since we joined him, that collection grew from about 100,000 specimens to its present roughly 550,000 prepared and 250,000 unspread specimens. The decision was made to gather material from throughout the world because we felt that revisionary studies done on groups from only part of their ranges were incomplete, and we wished to encourage a world view of butterflies and large moths. Another goal was to obtain collections in their entirety and not see them broken up as so many had been in the past. The vision of Art Allyn has been an inspiration to us, and we hope that the material he was responsible for gathering will be used for generations to come.

Thus far, almost everyone that I have mentioned in this tribute has been male. Consider the fact that the Rothschilds are and were an amazing lot, true "Renaissance men". The present Renaissance "man" of the Rothschilds is a woman: Miriam Rothschild has published a quarter of a million words on flea taxonomy, she has worked on plant-insect interactions, on intestinal worms, on mimicry in butterflies, on the behavior of sea gulls and has been involved with worldwide conservation efforts. Miriam Rothschild was educated basically at home, chiefly by her uncle Walter and his curators at Tring. She earned no university degree, but nonetheless is honored in scientific circles in

England and elsewhere. Her ability and tenacity have made her achievements possible.

The honor role of amateurs is long and distinguished. They have made and are making significant contributions to our chosen field. The next time you hear the statement, "He's only an amateur," realize that this should not be a pejorative; perhaps it is a tribute, since the person in question does not have to be paid to perform. All of us, amateurs and professionals alike, have something to give lepidopterology. The difference between amateur and professional is one of degree, rather than kind. In the final analysis, there is not "amateur science" and "professional science", there is only good science or poor science. Let us recognize that we all have something worthwhile to say, and we will all benefit from such understanding.

GENERAL NOTE

TRYON REAKIRT: A SEQUEL

In 1964 I wrote briefly about Tryon Reakirt, a Philadelphia entomologist of note during the 1860's (Brown 1964, J. Lepid. Soc. 18:211–214). He was a mystery man in his last years. All I knew earlier was that he had fled the country in early 1871. As a result, both his enterprises and his father's business filed for bankruptcy. I found the answer to his disappearance among newspaper clippings belonging to William Henry Edwards of Coalburgh, West Virginia.

One clipping is from the *Philadelphia Inquirer*, Wednesday, 8 February 1871. Reakirt had forged notes on large pharmaceutical houses to the tune of more than $110,000! An error in a date caused a bank clerk to go into the matter with the purported issuer. The fat was in the fire! Reakirt left town hurriedly, and ultimately got to Lima, Peru, where, apparently, he died of dysentery in late 1872 or early 1873.

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A NEW SPECIES OF *EPIDROMIA* (NOCTUIDAE) FROM FLORIDA

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ABSTRACT.   This preliminary study of the genus *Epidromia* Guenée (Ophiderinae: Noctuidae: Lepidoptera) describes a new species *E. fergusoni* and redescribes the type species *E. pannosa* Guenée.

Twenty species group names are included in the neotropical genus *Epidromia* Guenée (Ophiderinae). This genus is distributed in northern South America and throughout Central America and reaches its greatest diversity in the Antilles. Florida is its northernmost extension.

METHODS

Names applied to wing veins and markings correspond to Forbes (1923). The forewing length is measured from the base of the wing to the apex of the wing. The width is measured from the apex to the anal angle. The depth and width of the cleft of the ostium bursae is measured as shown in Fig. 1. All measurements correspond to the mean value, and the measurements in the parentheses are the range. The numbers in parentheses in the distribution section are USNM (United States National Museum of Natural History) genitalia slide numbers.

RESULTS

Epidromia is being redescribed since the original description is incomplete. The genitalia are described and illustrated for the first time.

Epidromia

Epidromia Guenée, 1852, *In* Boisduval and Guenée, *Hist. Nat. Insectes, Spec. Gén. des Lépid.* 7:325. Type: *Epidromia pannosa* Guenée, 1852, by subsequent designation (Berio, 1966. Annali Museo Civico Storia Naturale Giacomo Doria 76:57).

Penultimate segment of palpi upturned and longer than first and third segments together; ultimate segment ending in blunt point. Abdomen cylindrical, elongated; sternites more hairy than tergites; distal end appearing square-shaped in males and tapered in females (Figs. 3, 6 and 8) distal tergite square-shaped with membranous projections into seventh tergite, projections pointing medially; distal sternite with two sclerotized, long lobes connected by two smaller lobes (Fig. 2). Front legs stout with dense hairs. Wings entire, oblong; underside of wings having beige sheen with silky pubescence; peak of each scallop of adterminal line with immediately adjacent dot. Sacculus simple; uncus simple, widely angled distally; tegumen medially extended to point ventro-laterally; vinculum about as long as wide; vesica distally bilobed without cornuti (Figs. 4, 5 and 9, 10). Genital plate heart-shaped; ostium bursae cleft; no signa on corpus bursae (Figs. 7 and 12).
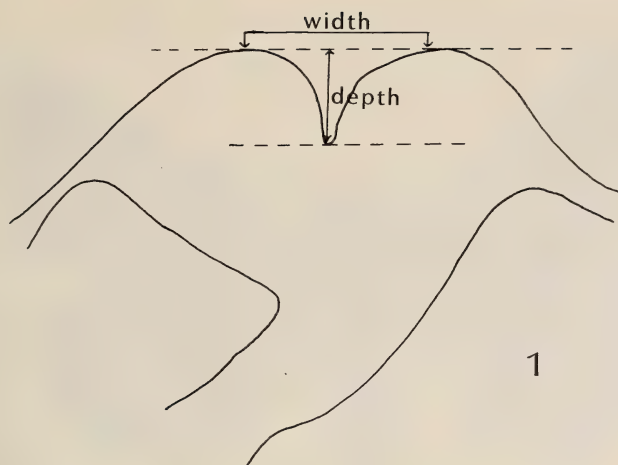
FIG. 1. Diagrammatic illustration of ostium bursa and measured distances.

Inspection of specimens and representative genitalia slides of genera believed to be closely related revealed that *Epidromia* is most closely related to *Itomia* Hübner. These two genera share an uncus that is simple, curved, and with a prominent spine at the distal end, and a costa on the valve that is strongly lobed. *Itomia* species more closely resemble *Epidromia* species from South America than those from Central America and the Antilles.

The type-species of *Itomia* is *Itomia lignaris* Hübner, by monotypy.

FIG. 2. Last abdominal segment of *Epidromia*.

FIG. 3. *Epidromia fergusoni,* holotype, male.

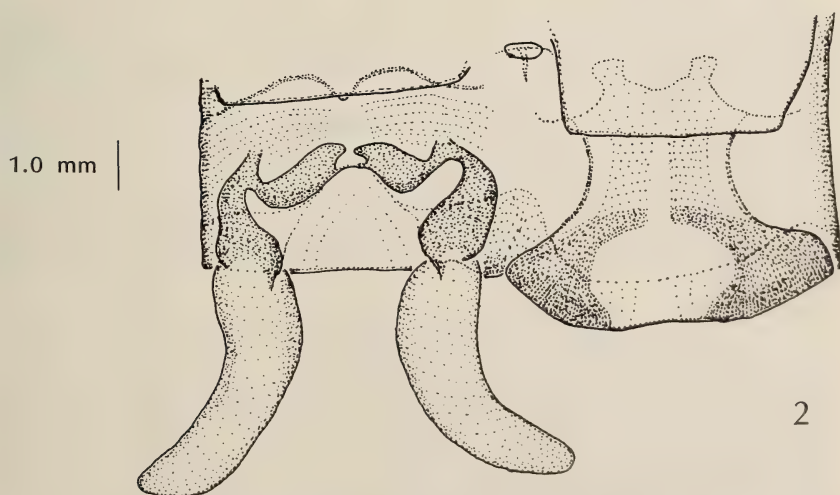The holotype is believed to have been destroyed (R. W. Poole, pers. comm.). The original description and illustration of *I. lignaris* are not adequate for identification of the species. The specimens at the USNM suggest that a complex of species is involved; therefore, a male and a female from the complex have been chosen for the purpose of the genitalia comparison (Female: Mizantlan, Mexico, slide no. 42,618; Male: Mizantlan, Mexico, slide no. 42,619) (Table 1).

Table 2 is simply a list of species group names currently placed in *Epidromia.* Some names are new combinations. Some of the names have been traditionally recognized as synonyms. Some species described by Walker from the Antilles are suspected to be synonyms; he described only females, and females are highly variable. Photographs of the Walker and Gueneé types from the British Museum were studied. There are three other new species that will not be described here. A full revisionary treatment is not feasible at this time because of the difficulties of assembling sufficient material and identifying all of the types.

Epidromia fergusoni Solis, new species

Male holotype. Scales of collar, thorax and abdomen brown with purplish tinge (purplish tinge may disappear with age). Third sternite of abdomen without large bristles (n = 7). Ground color of wings brown with purplish tinge. Forewing: Other margin undulated, invaginated at end of R_5, forming a peak at apex. Basal band brown (not visible); antemedial line light brown; triangular, chocolate brown area extending distally from base of antemedial line, terminating where postmedial line curves toward base of wing. Reniform spot gray (black, more obvious in older specimens). Postmedial line beige;

TABLE 1. Comparison of *Epidromia* and *Itomia*.

Structure	Epidromia	Itomia
Ultimate labial palp segment	blunt	pointed
Penultimate labial palp segment	four times as long as ultimate palp segment	two times as long as ultimate palp segment
Tergites and sternites of abdomen	sternites with more hair than tergites	sternites and tergites equally hairy
Distal end of abdomen	distal tergite square with membranous projections into 7th tergite bending dorsally; distal sternite with medial sclerotized area but not tubelike	distal tergite triangular with membranous projections into 7th tergite bending laterally; distal sternite with medial tubelike sclerotized area
Front legs	stout, with dense long hairs	slender, devoid of long hairs
Underside of wings	beige sheen with silky pubescence	yellow without silky pubescence
Dots at peak of each scallop of adterminal line	immediately adjacent	not immediately adjacent
Upper side of wings	variable	diagonal lines across the wings
Sacculus	simple	chitinized extension costad and extending distally
Tegumen	medially extended to a point ventrolaterally	simple
Vinculum	as long as wide	longer than wide
Uncus	not sharply angled	sharply angled distally
Vesica	distally bilobed	not distally bilobed
Genital plate	heart-shaped	rectangular, slightly longer than wide
Ostium bursae	with a definite cleft	cleft not definite

chocolate brown patch adjacent to postmedial line beginning at M_1 and extending distally to the apex of forewing. Adterminal line light brown, peak of each scallop with beige dot. Terminal line light brown (beige). Distal underside of wing without gold patch between M_1 and R_4. Forewing length 2.3 cm (2.2–2.4) (n = 25). Length/width ratio 1.5 (1.3–1.7). Hindwing: Outer margin round, area adjacent to margin light brown. Postmedial line same as in forewing; chocolate brown area extending from postmedial line to about halfway to base of wing (Fig. 3). Genitalia: Uncus enlarged at distal end; valve with thumblike process on saccular margin, distal end of valve expands into small, flaplike process; editum on costa round; longest lobe of vesica bifurcate, with short branch rounded and longer branch rounded; longer branch expanded at base and tapered to blunt point (n = 7) (Figs. 4, 5).

Female allotype. Scales of collar, thorax and abdomen brown. Ground color of wings brown. Forewing: Outer margin same as in male. Basal line (if visible) double, dark brown on inside, yellow on inside; median line dark brown (or absent). Reniform spot same as in male. Postmedial line double, brown on inside and yellow outside. Amount of beige in area between postmedial and adterminal line when present varies. Subterminal line yellow to brown with dot at peak of each scallop, terminal line brown. Forewing length 2.1 cm (1.9–2.2) (n = 25). Length/width ratio 1.5 (1.4–1.6). Hindwing: Outer margin same as in male. Line markings same as forewing, but basal line and antemedial line not visible (Fig. 6). Genitalia: Ostium bursae cleft, approximately 0.45 mm wide at distal end, depth of cleft 0.35 mm (0.28–0.40) (n = 4) (Fig. 7).

1.0 mm

4

1.0 mm

5
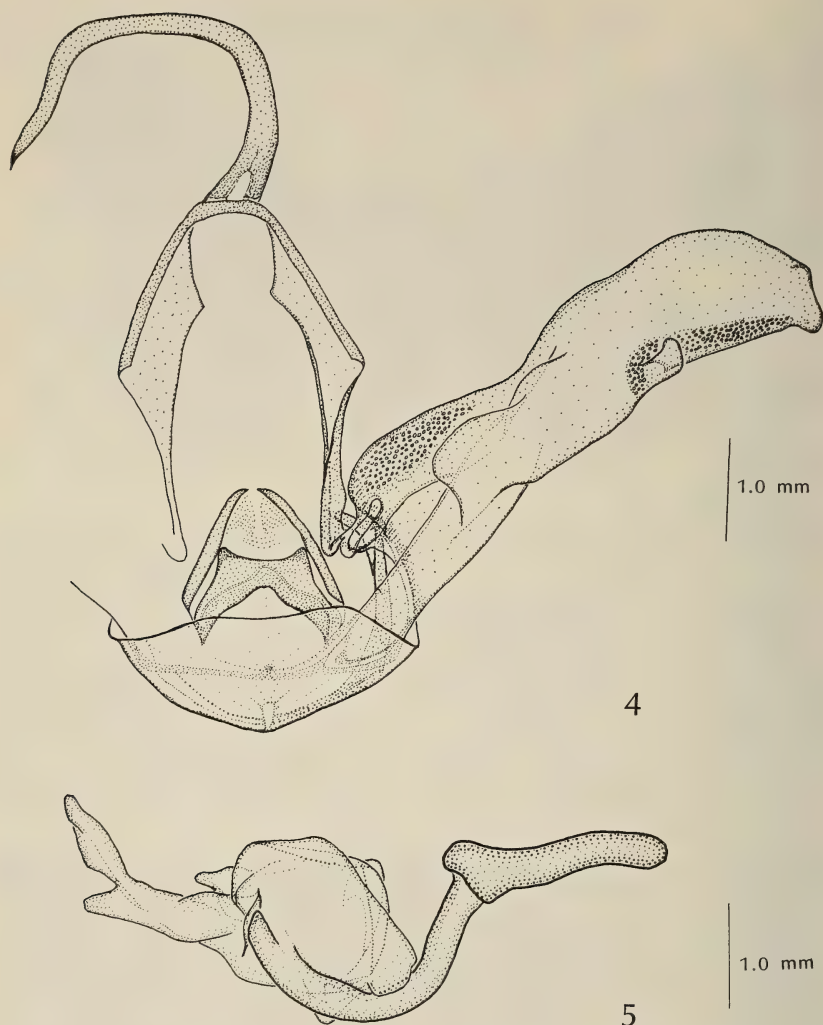
FIGS. 4 & 5.   Male genitalia of *Epidromia fergusoni*. **4,** Egmont, Fla., USNM slide 42,611; **5,** aedeagus, Miami, Fla., USNM slide 42,609.

Types. Holotype: Male (Fig. 3), University Reserve, Welaka, Putnam Co., Florida, 6 April 1972, D. C. Ferguson. Allotype: Female (Fig. 6), University Reserve, Welaka, Putnam Co., Florida, 6 April 1972, D. C. Ferguson. Paratypes: Six males, same locality and collector, USNM genitalia slide numbers 42,054, 42,614, 42,607; three females, same locality and collector. All specimens are deposited in the U.S. National Museum of Natural History, Washington, D.C.

Distribution. Other specimens used in this analysis were from the following localities in Florida: Miami, Glenwood, Ft. Myers, Ft. Meade, Dade City, St. Petersburg, Royal Palm State Park, Marcos Island, Lutz, Stemper, Indian River, Egmont, Ft. Lauderdale, Chokoloskee. Specimens with suspect data: Plainsfield, N.Y.; Jemez Springs, N.M.; Cuba.

Fig. 6.   *Epidromia fergusoni*, allotype, female.

Discussion

This is the Florida species that has been known in this country for nearly a century as *Epidromia delinquens* (Walker) (=*Ophiusa delinquens* Walker, 1858). However, Hampson (1913) referred *delinquens* to the synonymy of *Mocis repanda* (F.), a name that Hampson and

TABLE 2.   List of species group names in *Epidromia*. (Names in parentheses are the original combinations.)

Epidromia pannosa Guenée
E. zetophora Guenée
E. xanthogramma Wallengren
E. zephyritis Schaus
E. rotundata Herrich-Schäffer
E. consperata Dognin
E. poaphiloides Guenée
E. profana Walker
E. flavilineata (Hampson) NEW COMBINATION (*Thermesia flavilineata*)
E. glaucescens (Walker) NEW COMBINATION (*Thermesia glaucescens*)
E. lenis (Walker) NEW COMBINATION (*Thermesia lenis*)
E. antica (Walker) NEW COMBINATION (*Ophisma antica*)
E. arenosa (Walker) NEW COMBINATION (*Phurys arenosa*)
E. pedestris (Walker) NEW COMBINATION (*Phurys pedestris*)
E. profecta (Walker) NEW COMBINATION (*Poaphila profecta*)
E. saturatior (Walker) NEW COMBINATION (*Remigia saturatior*)
E. sigillata (Walker) NEW COMBINATION (*Thermesia sigillata*)
E. suffusa (Walker) NEW COMBINATION (*Thermesia suffusa*)
E. tinctifera (Walker) NEW COMBINATION (*Thermesia tinctifera*)
E. valida (Walker) NEW COMBINATION (*Ophisma valida*)

1.0 mm

7
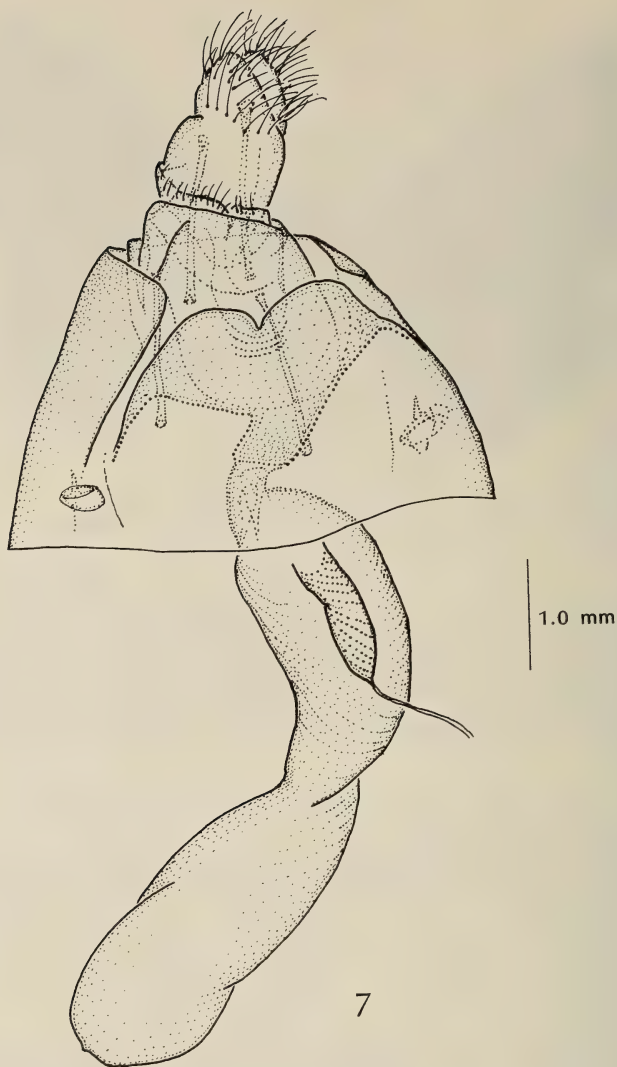
FIG. 7. Female genitalia of *Epidromia fergusoni*, paratype, Welaka, Fla., USNM slide 42,615.

other authors subsequently (but mistakenly) considered to represent the same species as *Mocis latipes* (Guenée). The type of *delinquens* has not been seen, but after reading the description by Walker, it is acknowledged that Hampson was correct in assigning it to the genus *Mocis* Hübner.

It should be noted that *E. fergusoni* is not the only species of *Epi-*

FIG. 8.   *Epidromia pannosa* Guenée, holotype, male.

dromia in Florida. A male specimen from Homestead of one unde-
scribed species and a male and a female from Big Pine Key of another
undescribed species have also been collected there and are now re-
corded from the continental United States for the first time.

E. *fergusoni* is named after Douglas C. Ferguson who collected the
type material.

Epidromia pannosa Guenée

Epidromia pannosa Guenée, 1852, *In* Boisduval and Guenée, *Hist. Nat. Insectes, Spec.
Gén. des Lépid.* 7:326.

TABLE 3.   Comparison of *E. pannosa* and *E. fergusoni*.

Structure	*pannosa*	*fergusoni*
Overall color	brown	purplish
Third sternite	with bristles	without bristles
Outer forewing margin	straight	undulated
Antemedial and postmedial line	double	single
Triangular, chocolate brown area extending distally from base of antemedial line	absent	present
Hindwing outer margin—male	angulate	rounded
Hindwing outer margin—female	rounded	rounded
Thumblike process on costa	absent	present
Short branch of bifurcated lobe of vesica	truncated	rounded
Cleft of ostium bursae	0.62 mm wide, 0.43 mm depth	0.25 mm wide, 0.35 mm depth
On underside of forewing—gold patch between M_1 and R_4	present	absent
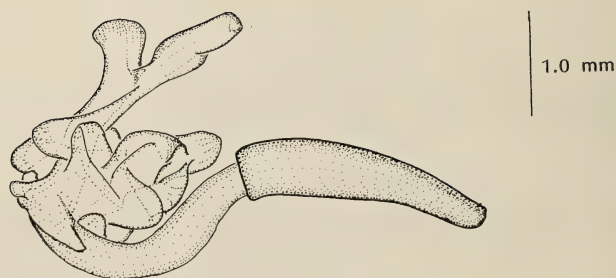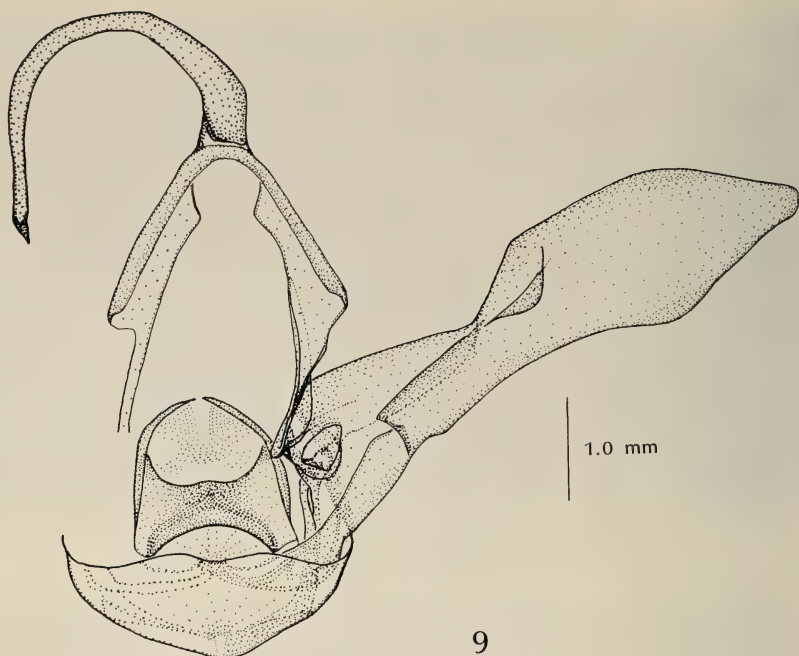
FIGS. 9 & 10.   Male genitalia of *Epidromia pannosa* Guenée. **9,** Rio Janeiro, Brazil, USNM slide 42,053; **10,** aedeagus, Venezuela, USNM slide 42,065.

Male. Scales of thorax and abdomen brown; head and collar dark brown. Third sternite with bristles (n = 4). Ground color of wings brown. Forewing: Outer margin not undulated. Basal band brown; antemedial line double, yellow on inside (may not be evident) and dark brown on outside. Median shade dark brown. Reniform spot outlined in dark brown, filled with gray (black or gray without outline). Postmedial line double, dark brown inside, yellow outside. Subterminal line faint, light brown (chocolate brown or lacking). Dark brown patch between subterminal and adterminal line extending from

FIG. 11. *Epidromia pannosa* Guenée, female.

M₂ to anal angle. Adterminal line dark brown, slightly scalloped; peak of each scallop with dark brown dot. Terminal line yellow (brown). (One specimen with vein lines dark brown.) Distal underside of wing with gold patch between M_1 and R_4. Forewing length: 2.3 cm (2.1–2.4). Length/width ratio: 1.6 (1.4–1.8) (n = 10). Hindwing: Outer margin slightly angulate at end of Cu_1; edge of wing above Cu_1 parallel to body. Area from apex to anal angle adjacent to outer margin dark brown (light brown or no shading). Median shade, postmedial and subterminal line same as forewing (Fig. 8). Genitalia: Uncus enlarged at distal end; editum on costa round; vesica with longest lobe bifurcates, short branch truncate, long branch expanded at base, tapering to blunt point (n = 4) (Figs. 9 and 10).

Female. Since Gueneé did not describe the female of this species, the following description of a female believed to represent the same species from Aroa, Venezuela is provided. Three males of this species were collected at Aroa, Venezuela and all four (three males and one female) have the same label information. Scales of head, collar, thorax, and abdomen same color as male. Ground color of wings same as male. Forewing: Median line dark brown. Reniform spot same as male. Postmedial line same as male; subterminal line beige. Length: 2.1 cm. Length/width ratio: 1.7 (n = 1). Hindwing: Outer margin round. Median line, postmedial line and subterminal line same as forewing (Fig. 11). Genitalia: Ostium bursa cleft, approximately 0.62 mm wide at distal end, depth of cleft 0.43 mm (n = 1) (Fig. 12).

Types. The holotype, in the British Museum of Natural History, is a male with no label data other than "Bresil." A photograph of the type specimen taken by R. W. Poole was used in this description.

Distribution. Aroa, Venezuela: one female (42,115) and three males (42,065); Edo. Zuela, Venezuela: three males; Rio Janeiro: one male (42,053); Castro, Parana: one male (42,057); Merida, Mexico: one male (42,069); Tamazunchale, Mexico: four males; Mazatlan, Mexico: one male (42,056); Poza Rica, Mexico (42,072). All specimens examined are in the collection of the U.S. National Museum of Natural History.

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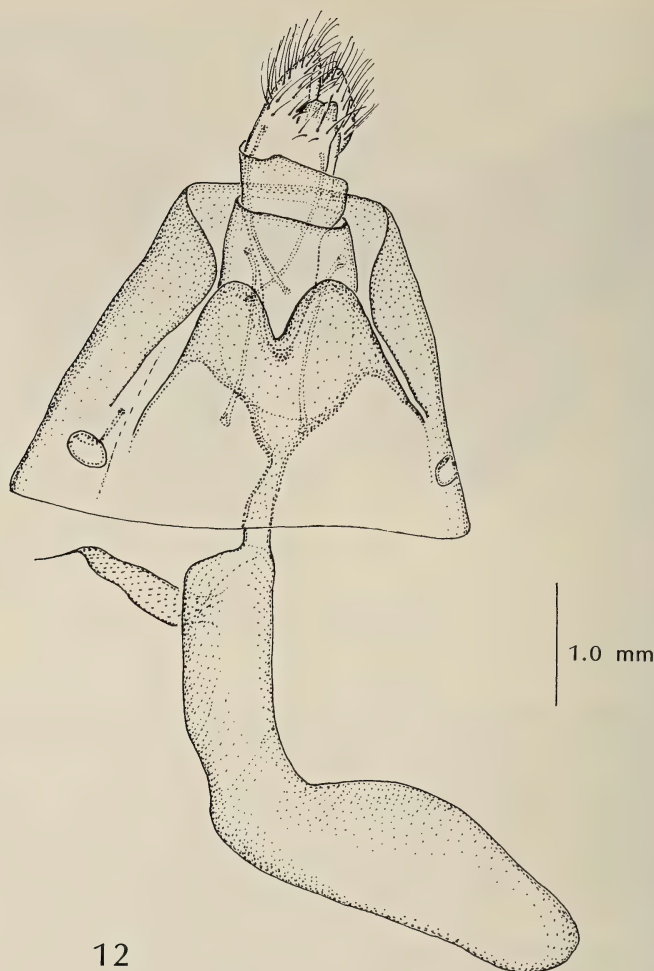
Fig. 12. Female genitalia of *Epidromia pannosa* Guenée, Venezuela, USNM slide 42,115.

Discussion

J. G. Franclemont and E. Todd (1983) mistakenly synonymized *pannosa* and *poaphiloides*. This synonymy was probably based on notes by Hampson that were never published and transferred from the British Museum of Natural History to the U.S. National Museum of Natural History. *E. poaphiloides* was described from Cayenne, French Guiana by Gueneé in 1852. The type of *poaphiloides* is believed to have been destroyed or lost (R. W. Poole, pers. comm.). An illustration of the type

is not available. After reading the written description, it is quite obvious that *poaphiloides* is not *pannosa*. A number of specimens of *poaphiloides* from French Guiana and British Guiana (Guyana) can be found at the U.S. National Museum of Natural History.

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THE LARVA AND PUPA OF *LYCOREA PIETERI* LAMAS (DANAIDAE)

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ABSTRACT. The larva and pupa of the danaid *Lycorea pietri* Lamas is described and figured for the first time. It differs most markedly from the larvae of other danaids in having only a pair of tentacles in front and none in the rear. The food plant is *Carica papaya* (Cariaceae).

During the last quarter of the 18th Century there was a gifted architect in northern Haiti who was also a naturalist 200 years ahead of his time. His work is unknown to biologists even though he painted from life accurately hundreds of Haitian animals and plants. Most of his subjects did not become known to binomial taxonomy until two generations later. He is unpublished, except that apparently Deshayes pirated some of his work and sent it to Buffon (Wetherbee, in press). Not only did he paint some 50 Lepidoptera, but he reared them from larvae and depicted the early stages and named several of them from their food plants.

He was "M. de Rabié, marechal de camp, ingenieur en chef de la parties du nord de St. Domingue" and resided at Cap Haitian from at least as early as 1752 to about 1784 and died in Paris in 1785. His first insects were drawn in 1766. Folios of his work are now in the Blacker-Wood Library of McGill University. Through the courtesy of Miss Eleanor MacLean, McGill Librarian, I have been privileged to publish Rabié's zoological subjects (Wetherbee, 1985a).

Rabié reared *Lycorea pieteri* Lamas (formerly called *L. ceres* Cramer, 1779) and depicted the larva, pupa, shed "robe" and imago. He called the larva "chenille de papayer (food plant: *Carica papaya* of the Caricaceae) and the adult "le noeud de ruban" (ribbon-bow). This is *L. pieteri cleobaea* Godart, 1819, the type-specimen of which was collected, undoubtedly, by Antonio Gonzales of the covert Baudin voyage to Hispaniola in 1799.

Most of the larvae of Lepidoptera drawn by Rabié were those of moths, especially of Sphingidae (Wetherbee, 1985b). Only four other butterfly species of the 36 species illustrated by Rabié (Wetherbee, 1985a) show early stages: *Danaus plexippus*, *Colobura dirce*, *Siproeta stelenes* and *Dione vanillae*.

As can be seen from Fig. 1 (the black and white reproduction hardly does justice to the beauty of Rabié's colored painting), the larva (perhaps fourth instar) is danaid in character, but unlike *Danaus*, which has pairs of both anterior and posterior fleshy tentacles, and unlike
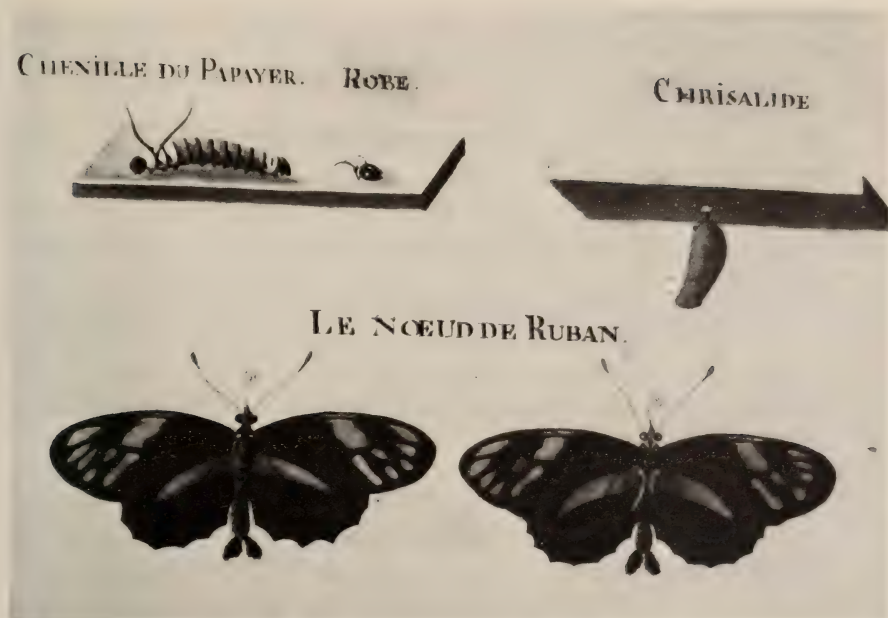
CHENILLE DU PAPAYER.   ROBE.   CHRISALIDE

LE NŒUD DE RUBAN.

FIG. 1. *Lycorea pieteri* Lamas (*L. p. cleobaea* Godart, 1819) life history as painted by Rabié in Haiti in 1782.

Anetia which has none, *Lycorea pieteri* has only a pair of anterior tentacles. These are slightly longer than those of *Danaus plexippus*. The larva is smooth, about the same size as *D. plexippus*; both the head and posterior segment are black; the thoracic segments are white, followed by seven golden-yellow segments and then one white next to the last segment in front of the black tail-end. The narrow black bands, one at the anterior of each segment, have short, black, single, lateral, oblique, dash-like marks pointing backwards and downwards.

The hanging pupa is shown by Rabié in its lateral aspect only. It is similar in texture, size and shape to *D. plexippus* (but without the ridge) and is golden yellow with black bump-dots running in two arched lines on the sides, a few on the anterior parts, one prominent "occipital" bump-dot and two anal ones. The cremaster is black and contrasts sharply with the white web.

One must pause to consider that this excellent work was accomplished contemporary with Linnaeus' 12th edition of the Systema Naturae in a country which has had essentially no entomological research up to the present time. If we consider that Audubon was somewhat of a pioneer and hero, certainly Rabié was even a greater one.

Since viewing Rabié's pictures, I have had the good fortune in No-

vember of finding many of the larvae of this species in Restauración, República Dominicana feeding on *Carica papaya*. The early stages are only slightly tinged with yellow. The fifth instar does not have the posterior segments white as shown by Rabié, but the thoracic segments tend to be whitish. The black tentacles are 15 mm in length, and the larva is about 40 mm. The ten narrow, black bands on the anterior of each segment send a spur toward each black spiracle and sometimes include it. The ultimate yellow segment has only three black dots representing the band. There are a pair of yellow eye-spots on the small black ultimate black segment. Both in Rabié's illustration and in life, it is easy to mistake the tail for the head in the resting caterpillar.

The pupa is always suspended from the midvein of the green lechosa leaf about midway along the length of the leaf. It is dull waxen-yellow. The black dots run in a mid-dorsal series, a dorso-lateral series, and there is an arc of elongated dots on the wing following the curvature of the wing and an isolated black dot in the middle of the wing. As shown by Rabié, there is a pair of black bumps on the body near the base of the cremaster.

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LIFE HISTORY AND HABITS OF *EXOTELEIA ANOMALA* HODGES, A PONDEROSA PINE NEEDLE MINER IN THE SOUTHWESTERN UNITED STATES (GELECHIIDAE)

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ABSTRACT.   *Exoteleia anomala*, the larvae of which mine needles of ponderosa pine in Arizona and New Mexico, has a one-year life cycle similar to that of several species of needle-mining *Coleotechnites*. Each larva requires two needles to complete development. When numerous, larvae can cause highly visible foliage damage, but outbreaks do not appear to persist.

In summer 1977, I reared an undescribed species of *Exoteleia* (Gelechiidae) from foliage of ponderosa pines, *Pinus ponderosa* Dougl. ex Laws., near Silver City, Grant Co., New Mexico. In 1978, entomologists with the USDA Forest Service, Southwestern Region, Albuquerque, New Mexico, reported a needle miner infestation in ponderosa pines from an area near Show Low and Pinetop, Navajo Co., Arizona, some 90 km NW of Silver City. No moths were obtained at that time, but a resurgence of the population in 1981 provided material for study; it too was *E. anomala*. Collections and observations in 1981 and 1982, reported here, have made it possible to outline the species' life history and habits.

METHODS

Collections of foliage representing at least two years' growth were made 21 October 1981, and 4 March, 6 April, 10 May, 22 June, 12 July, and 25 August 1982 for the 1981–82 generation, and a single collection from the 1982–83 generation was obtained on 11 November 1982. Life history events and larval habits were recorded following examination of the foliage, and sufficient numbers of larvae were preserved to permit determination of instars. Adult voucher specimens are deposited in the U.S. National Museum of Natural History.

DESCRIPTION

The adult is described in detail by Hodges (1985). Briefly, it is a small, fragile moth, forewing length 4–5 mm, with a whitish head, mottled gray-brown to black and white forewings, and mottled brown and whitish abdomen. The hindwings are grayish, and have fringes of long hairs.

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First-stage larvae are tan, with light brown head capsules and pro-
thoracic and anal shields. Instars 2, 3, and 4 are brown, with dark
brown to black head capsules and anal shields. Prepupal fourth-stage
larvae are dark brown to almost black.

Its appearance, coupled with its needle-mining habit, can lead
nonspecialists to confuse this species with well known pine needle min-
ers in the genus *Coleotechnites.*

LIFE HISTORY AND HABITS

Exoteleia anomala has a one-year life cycle. The moths fly and
oviposit in midsummer, and the larvae overwinter. Pupation takes place
in the mined needles. The life history is similar to that of a more
northern but potentially sympatric species of needle miner *Coleo-
technites ponderosae* Hodges & Stevens (Stevens 1973, Hodges & Ste-
vens 1978), and an undescribed species of *Coleotechnites* from *Pinus
jeffreyi* Grev. & Balf. in southern California (Luck 1976). However,
larval habits of *E. anomala* are different.

Adults fly in June and July. Eggs were not seen, but they may be
laid in old mined needles as with *Coleotechnites* pine needle miners
(Stark 1954, Struble 1972, Stevens 1973), or in other locations near
susceptible new foliage.

Larvae readily colonize foliage of the current year's growth, in con-
trast to *C. ponderosae* larvae, which seem to prefer older foliage (Ste-
vens 1973). Examination of shoots from 12 heavily infested trees col-
lected 21 October 1981 showed that 72% of the new (1981) needles
had been invaded, as had 65% of the 1980 foliage. How much of the
damage to 1980 foliage resulted from mining by the 1981 generation
was not determined; certainly some was attributable to the 1980 gen-
eration. A collection of 14 1981 shoots, made in July 1982 after all
larval feeding had ended, showed that only 8% of the needles had
escaped infestation.

Larval head capsule measurements indicate four instars (Fig. 1).
Each larva utilizes two needles to complete development. First instars
enter the first needle in late summer, molt, and remain there as second
instars until spring. Most of the larvae in the 4 March 1982 collection
appeared to have only recently arrived at the second needle. Larvae
enter the first-mined needles in the middle third of the needle. This
mine is short, only 1–2 cm; the part of the needle distad of the mine
soon dies and fades. Larvae normally enter the second-mined needle
within 1 cm of the tip, and more of the second needle is excavated. A
set of 28 fully developed mines (from which adults had emerged)
averaged 5.7 cm long (SD = 1.2 cm). The larvae cut small holes in the
needle surface for disposal of frass; these are covered with silk from
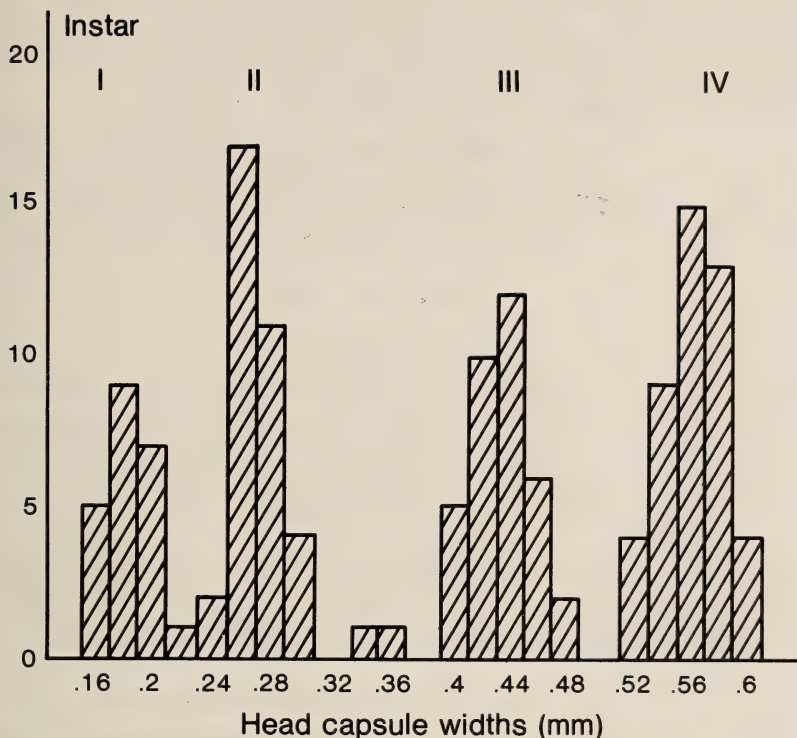
FIG. 1.   Head capsule measurements (n = 138) of *Exoteleia anomala* larvae.

within after they are no longer needed. There is usually only one needle miner per needle, but more than one larva per needle does occur. When this happens, normal entry locations are altered. Larvae located distally to others in a single needle do not complete development, and may move to another needle.

Pupation, as in the well known *Coleotechnites* pine needle miners and some species of *Exoteleia*, takes place within the last mined needle. The larva cuts a hole in the needle surface to allow for adult exit. The hole may be at either end of the mine. Pupae are dark brown to black, cylindrical, and 5.5 to 6.0 mm long. They are usually found 1 cm or more back from the exit hole, head pointing toward it.

POPULATION FLUCTUATIONS AND EFFECTS OF LARVAL FEEDING

Although heavy larval feeding can cause many needles to die, no permanent tree damage has been reported. This may be due to the

fact that outbreaks of *E. anomala* appear not to persist. For example, population densities were high enough to attract attention in Arizona in 1978, but no infestation was reported during the next 2 years. Larval numbers in 1981 appeared to decline markedly at the time of transfer from first- to second-mined needles. This may be a time in the insect's life cycle when it is particularly vulnerable.

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BIOLOGY AND IMMATURE STAGES OF *HEMILEUCA DIANA* AND *H. GROTEI* (SATURNIIDAE)

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ABSTRACT. The primary host plant of *Hemileuca diana* in Arizona is *Quercus oblongifolia*, Mexican blue oak. Adult flight records extend from August to late November, but peak emergence is in October. The primary host plant of *H. grotei* in central Texas is *Quercus fusiformis*, live oak. Adult *grotei* fly from late October to December. Adult *Hemileuca grotei* from New Mexico are similar to those from Texas. Immature stages and adults of both species are illustrated, as is the holotype of *H. diana*. Although closely related, hybrid matings between these two species do not produce viable ova.

Hemileuca diana Packard

Hemileuca diana is locally abundant in the mountains of Arizona but frequently difficult to locate or capture. Presently *diana* is known from Arizona, New Mexico, Colorado, and Sonora, Mexico. Although there are two old Texas records, the data are incomplete and probably in error (Ferguson 1971). *Hemileuca diana* is associated with the montane oak habitat above 1,100 m (Fig. 1b) and is undoubtedly widespread from northern Mexico to Colorado. Because of its similarity to *H. grotei* Grote & Robinson, the two species have been confused in the literature, making it difficult to accurately determine the extent of either species distribution.

The specimens of *diana* illustrated by Ferguson (1971) are typical in appearance but slightly smaller than average. The forewing length of males from southern Arizona ranges from 23 to 28 mm, $\bar{X} = 24.3$ mm (N = 34); females from 27.6 to 31.5 mm, $\bar{X} = 29.9$ mm (N = 14). The fore- and hindwing ground color of the female is black or dark brown. The forewing of the male varies from brown to dark brown, while the hindwing is dark brown. Both sexes have a cream-colored medial line which passes distal to the forewing discal spot (Figs. 2a, b, i, j). The genitalia of a male *diana* was illustrated by Ferguson (1971) but was accompanied with *grotei* locality data. Ferguson (pers. comm.) re-examined the specimen and confirmed its identity as *diana*.

Minor geographical variation has been observed among the males in southern Arizona. This might be expected since many of the mountain ranges *diana* inhabits are isolated by distance and habitat. Males from the Huachuca Mts. in Santa Cruz and Cochise counties exhibit the most contrast between fore- and hindwing coloration (Fig. 2a). Specimens from the Santa Catalina Mts., Pima Co. (Fig. 2b), and Graham Mts., Graham Co., have forewings usually, but not always, darker than those from the Huachuca Mts. Specimens from the Chiricahua Mts.,
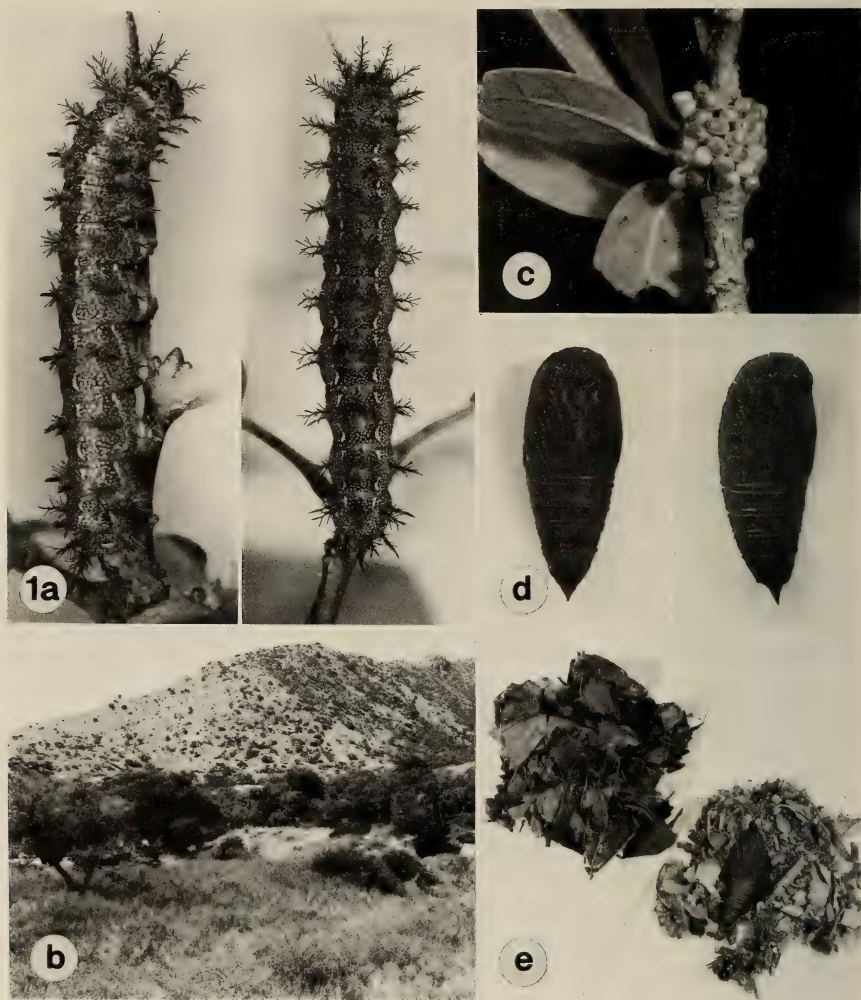
FIGS. 1a–e.   Immature stages of *Hemileuca diana*. **a,** mature larvae, lateral and dorsal view; **b,** *H. diana* habitat, Pima Co., Arizona; **c,** egg ring on *Quercus oblongifolia*; **d,** ventral and lateral view of male pupa; **e,** pupal chamber.

Cochise Co., are slightly smaller and have the least contrast between fore- and hindwings. Even though subtle differences are noted, overlapping phenotypic variation among these populations makes the application of subspecific names unwarranted.

Adults from central Arizona (Figs. 2c, d) appear intermediate to *diana* and *grotei*. The cream colored medial forewing line is thin and disrupted by the discal spot, as in *grotei* (Figs. 2e, f, g), but the hind-
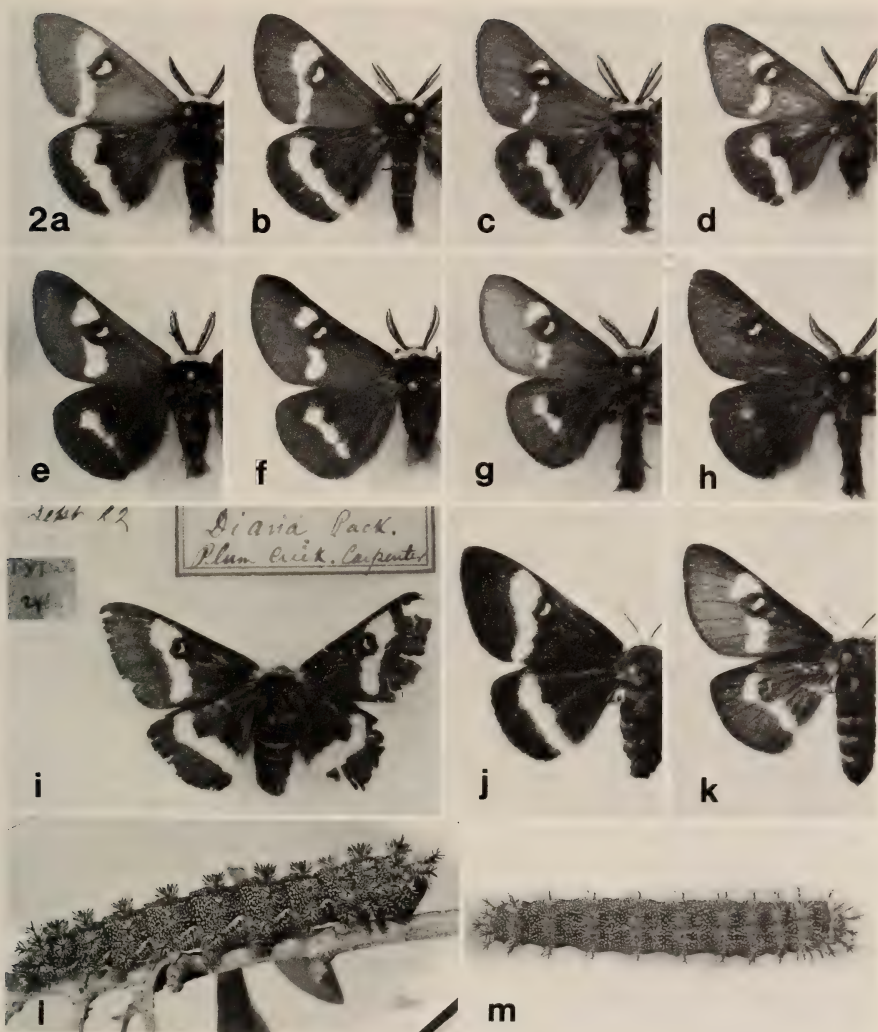
FIGS. 2a–m.   Adults of *Hemileuca diana*, *H. grotei*, and immature stages. **a,** *H. diana* ♂, Huachuca Mts., Cochise Co., Az; **b,** *H. diana* ♂, Santa Catalina Mts., Pima Co., Az; **c,** *Hemileuca* sp. ♂, Oak Creek Canyon, Coconino Co., Az; **d,** *Hemileuca* sp.? ♂, Sunflower, Maricopa Co., Az; **e–h,** *H. grotei* ♂♂, Burnet Co., Tx; **i,** Holotype ♀, *H. diana*; **j,** *H. diana* ♀, Santa Catalina Mts., Pima Co., Az; **k,** *H. grotei* ♀, Burnet Co., Tx; **l,** mature *H. grotei* larvae, lateral view; **m,** mature *H. grotei* larvae, dorsal view (larvae from Burnet Co., Tx).

wing medial line is well developed, and continues to the anal wing margin, as in *diana* (Figs. 2a, b). The forewing length of the six males examined ranged from 21 to 24 mm. The genitalia are variable but have distinct characteristics. I reared one larva collected on scrub oak

in Oak Creek Canyon, Coconino Co., Arizona. The mature larva was grayish, the intersegmental area was brown, and appeared distinct when compared to *diana* larvae from southern Arizona, and more similar to *grotei* larvae from Texas. Females from this population have not been available for examination. The material from central Arizona appears distinct and may represent an undescribed taxon.

An examination of the *diana* holotype from Plum Creek, Colorado (Fig. 2i) confirms that there is no obvious difference between the type and females from southern Arizona (Fig. 2j). Ferguson also noted that the type agreed well with material from southern Arizona. Therefore, if a new name is proposed it should be applied to the central Arizona phenotype.

Biology

In southern Arizona, the flight period of *diana* extends from mid-September to late November, with the peak near mid- to late October, but this may vary from one mountain range to the next by as much as three weeks. Adults emerge in the morning and usually mate before 1200 h. Male flight activity usually occurs between 0930 and 1630 h. Females oviposit during the afternoon. The flight of the female is slower, more straight, and higher among the oaks than that of the male, which is rapid, erratic, and usually within 3 m of the ground.

Females deposited 80 to 140 ova in two to four separate egg rings near the tips of the branch close to the leaf clusters (Fig. 1c). Field collected egg rings contained 25 to 65 greenish-gray ova. The eggs overwinter, and larvae usually hatch during April or early May.

The larval hostplant in Pima, Santa Cruz, Graham and Cochise counties, is Mexican blue oak, *Quercus oblongifolia* Torr. Michael J. Smith (pers. comm.) indicates that larvae are occasionally found on Emory oak, *Q. emoryi* Torr. Early instar larvae are black and feed gregariously. During the first two or three instars, larvae prefer developing flower buds and new leaves. If disturbed fourth instar larvae release their grip, fall to the ground, and disperse.

Mature larvae feed singly and do not drop to the ground when disturbed. Some larvae have six rather than five instars but are identical in appearance to those with one less. The mature larva is gray with a distinctly dark gray dorsal area, and purple intersegmental areas (Figs. 1a, b). Larvae from the Santa Catalina and Huachuca Mts. were reared on five different occasions and mature larvae from the Graham Mts. were examined. Within these three populations, the larval phenotype is uniform. Pupation usually occurs in early June but James S. McElfresh (pers. comm.) has found mature larvae during early September.

Larvae pupate under leaf litter, where they construct a small chamber of debris tied together with silk (Fig. 1e).

On four different occasions a total of seven *diana* females from Arizona attracted and mated with wild male *grotei* in Texas. Collectively, the *diana* females deposited nearly 900 ova, but none hatched. Dissection of the hybrid ova about one month after pure *diana* and *grotei* ova hatched revealed that only a few contained dead, partially developed embryos; most ova appeared to be infertile. The high degree of genetic incompatibility between these two taxa leaves no doubt that they are distinct species. Females of both *H. juno* (Packard) and *H. electra* (Hwy. Edwds.) can be used to attract *H. diana* males (Tuskes 1984). A cross between an *electra* female and a male *diana* produced fertile ova, but upon hatching the larvae refused to feed on host plants of either species. Females of *electra* will also attract and mate with male *H. eglanterina* (Boisduval) but only infertile ova are produced (Collins & Tuskes 1979).

Larval Description

The larval description is based on 26 larvae reared to maturity from ova collected in 1982 by Mike Smith and the author, at Molino Basin, Santa Catalina Mts., Pima Co., Arizona. Preserved larvae are in the author's collection.

First instar. Head: Black, diameter 0.7 mm. **Body:** Length 6 mm, width 1.4 mm. Ground color black. Dorsal area black, lateral and ventral surfaces dark brown to black. Dorsal and dorsolateral scoli forked near apex, one seta on each fork. All scoli black. True legs and prolegs black.

Second instar. Head: Black, diameter 1.5 mm. **Body:** Length 10–11 mm, width 2.0–2.2 mm. Similar to first instar except for a small red dot between the dorsolateral and lateral scoli on abdominal (A) segments A1 and A7.

Third instar. Head: Black, diameter 2.1–2.3 mm. **Body:** Length 19–20 mm, width 4.0–4.2 mm. Ground color black. All scoli black and branched. Lateral surface with traces of 3 incomplete lines extending length of larva. Line 1 incomplete, undulating, and white, touching lateral scoli and extending length of larva. Line 2 thin, white dash just anterior of dorsolateral scoli on each abdominal segment. Line 3 thin, white, and broken by black segmental area, passing just ventral to dorsal scoli. Spiracles, prolegs, and true legs black.

Fourth instar. Head: Black with short white secondary setae; diameter 3.5–3.9 mm. **Body:** Length 32–37 mm, width 9.5–11 mm. Ground color black. Three broken white lateral lines extend length of larva. Line 1 passes between lateral scoli and is well defined only on posterior portion of each segment. Line 2 passes between dorsolateral scoli; prominent on posterior of each segment. Line 3 passes mid-way between dorsolateral and dorsal scoli; broken by intersegmental area. Area between line 1 and ventral surface gray; between lines 1 and 2 (spiracular area) black; between lines 2 and 3, dark gray. Dorsal and mid-dorsal area black. All scoli black with white or hyaline colored spines. Short white secondary setae extend from white or light gray pinacula on lateral and dorsal surfaces. Prominent red-orange dot occurs between lateral and dorsolateral scoli on A1; similar but smaller dot on A7. Spiracles black. All shields black. Inner portion of proleg and ventral surface brown. True legs black.

Fifth instar. Head: Dark brown with numerous white secondary setae; diameter 5.1–5.4 mm. **Body:** Ground color dark gray. Length 47–58 mm, width 7.5–10 mm. Dorsolateral, lateral and sublateral scoli with black shafts and black and gray spines; base of shaft ringed with gray. Dorsal metathoracic scoli to A8 rosette type with black tips and dark gray base. Pro- and mesothoracic dorsal scoli enlarged. Two prominent light gray lateral lines extend length of larva and divide dorsal and lateral areas. Line 1 undulating, and passes between lateral scoli. Line 2 passes just ventral to dorsolateral scoli and is interrupted by maroon intersegmental area. Lateral segmental area between lines 1 and 2 gray with numerous light gray pinacula which may contain short white secondary setae. Dorsal area black with fewer light gray pinacula than lateral segmental area. Intersegmental area between lateral and dorsolateral scoli black or dark gray. Dorsal intersegmental area maroon. Ventral surface light brown to flesh with light gray pinacula in intersegmental area. Prominent shiny orange spot occurs posterior and near to spiracles on A1 and A7. Thoracic shields black. True legs dark brown. Prolegs gray with dark gray shields. Spiracles orange.

Hemileuca grotei Grote & Robinson

Until recently, little information was available on the biology of *Hemileuca grotei*. Ferguson (1971) illustrated both *grotei* and *diana*, and pointed out major differences in adult morphology, wing pattern, and distribution. Kendall and Peigler (1981) provided additional information on the distribution and flight period of *grotei* in Texas. No mention has been made of the extreme phenotypic variation found in the adults, and only a partial description of the immature stages has been published.

Most males and females have a well defined white medial band on the forewing interrupted by the dark discal spot. On the male hindwing, the white medial line is usually widest between M1 and M2, then narrows and terminates between Cu1 and 2A (Figs. 2e, f, g). In females, the medial hindwing line is more developed, seldom strongly tapering, and extends beyond 2A to the anal margin of the wing (Fig. 2k).

Some adults are almost entirely black, with only the white bar in the center of the forewing discal spot present. Others have only a trace of the hindwing medial line (Fig. 2h). Of approximately 400 males examined, 3 to 7% represent the dark phenotype. The occurrence of a dark phenotype is not uncommon in many *Hemileuca* species (Tuskes 1984). Normally, the ground color of the male is dark brown to nearly black. Sometimes the base of the forewing is dark gray, and the medial and distal portions are light gray (Fig. 2g). The ground color of the female is dark brown to black. Forewing length of males from Inks Lake, Burnet Co., Texas, ranged from 22.0 to 25.3 mm, $\bar{X} = 24.2$ mm ($N = 30$); females varied from 26.0 to 29.4 mm, $\bar{X} = 28.1$ mm ($N = 30$).

In addition to Texas, *Hemileuca grotei* occurs in New Mexico. Richard Holland collected a series at Dome Lookout (Sandoval Co., X-11-

84, elev. 2,460 m), and in the northwestern corner of the state at Fort Windgate (McKinley Co., IX-30-1975). The average forewing length of the Dome Lookout males is identical to that of central Texas populations. There are subtle differences in coloration and the frequency of various phenotypes between central Texas and New Mexico material examined. In 38% of New Mexico males (N = 18), the white medial hindwing line is absent; thus the wing is solid black. Further, there does not appear to be a relationship between the presence or absence of the medial hindwing line and the development of the forewing medial line. In Texas populations, if the hindwing line is reduced or absent, the forewing line also tends to be reduced. One specimen exhibits the same grayish scaling on the forewing as illustrated in Figure 2g. The only female examined was identical to those from central Texas.

Biology

Both males and females are active day flyers. The flight season in central Texas extends from October to early December, but peak emergence is near mid- to late November. Local climatic conditions significantly influence duration and extent of daily adult flight. In late November 1982, 26 males were collected during a one-day trip. The high temperature for the day was 14.4 C, with light rain, strong gusty winds, and 85% cloud cover. The first males were observed at 1020 and the last at 1430 h. During a trip in 1983, conditions at the same location were clear with a high of 25 C and light winds. At that time males were very abundant, and in flight from 0910 to 1800 h. Females were observed and captured in flight from about 1200 to 1800 h.

Newly emerged larvae are black and feed gregariously. The dark coloration may aid thermoregulation and increase activity during the early spring. Like those of *H. diana*, fourth instar *grotei* larvae tend to drop from the branch if disturbed. During the late fourth and fifth instars, larvae exhibited almost equal preference for flowers or leaves. The natural larval hostplant is *Quercus fusiformis* Small. Kendall and Peigler (1981) reported that *Q. havardii* Rydberg × *Q. stellata* Wangenheim, *Q. texana* Buckley, and *Q. marilandica* Muenchhausen are also utilized, but to a lesser extent. Mature larvae measure 39 to 48 mm in length, and have a gray ground color. The dorsal surface is darker than the lateral surface and the intersegmental area is reddish brown (Fig. 2l, m).

Before pupation the larva appears to darken, shrink in size, and the intersegmental color becomes less prominent and the light yellow pinacula become light gray. Larvae wander from one to three days before constructing a loosely woven cocoon in the leaf litter. Seventy-

seven larvae were reared from ova to maturity; 43 were males and 34 were females. All appeared to have five larval instars, and exhibited little variation. As with *H. diana*, most *grotei* pupae produce adults the same year, but both species have the ability to spend two years in the pupal stage.

Larval Description

The description is based on 77 larvae reared to maturity from ova deposited by a female collected by the author at Inks Lake State Park, Burnet Co., Texas.

First instar. Head: Black, diameter 0.8 mm. **Body:** Length 6 mm, width 1.2 mm. Ground color black to dark brown. Dorsal pro- and mesothoracic scoli forked at tip. Metathoracic scoli forked or spiked, remaining scoli spikelike. All scoli black with light colored setae extending from apex of each shaft. Ventral surface dark brown to black. True legs and prolegs black.

Second instar. Head: Black, diameter 1.4 mm. **Body:** Length 10 mm, width 1.8 mm. Similar to first instar with one exception: A small orange patch occurs between the dorsolateral and lateral scoli of A1.

Third instar. Head: Black, diameter 1.8–2 mm. **Body:** Length 18–19 mm, width 3.4 mm. Ground color black. Pro- and metathoracic scoli enlarged; shaft black, spines yellow and black. Dorsal abdominal scoli black; spines yellow with black tips, rosette pattern developing. Dorsolateral, lateral and sublateral scoli black with black spines. Trace of 3 incomplete light yellow lines extend length of larva, lines variable. Line 1 undulating, subspiracular, extending from A1 to A9, and touching base of each lateral scolus. Line 2 broken, consisting of dots passing along base of dorsolateral scoli. Line 3 often well developed, extending from T2 to A8, passing just ventral of dorsal scoli, often disrupted by intersegmental area. Orange dot on A1 and smaller dot on A7, both set between dorsolateral and lateral scoli. True legs, prolegs, and spiracles black. Small yellow pinacula occur on all segmental areas, including ventral surface.

Fourth instar. Head: Black, diameter 3.0–3.4 mm. **Body:** Length 31–33 mm, width 5 mm. Ground color black. Dorsal thoracic scoli T1 and T2 elongated, with black shafts and gold spines. Dorsal abdominal scoli rosette type with black base and gold spines, and light brown to black tips. Dorsolateral, lateral and sublateral scoli with black shaft and gold spines. Three incomplete light yellow lines extend length of larva, some may be poorly developed. Line 1 undulating, subspiracular, connecting base of all abdominal lateral scoli. Line 2 lightly marked, sometimes absent, in line with dorsolateral scoli on segmental area. Line 3 passes just ventral to base of dorsal scoli; interrupted by black intersegmental area. Body covered with small light yellow pinacula with a short hyaline setae extending from each. Mid-ventral surface dull orange-brown. Spiracles orange. Prominent orange dot occurs between lateral and dorsolateral scoli of A1; smaller dot similar in color and location on A7. True legs and prolegs black.

Fifth instar. Head: Black with short white secondary setae, diameter 4.6–5.0 mm. **Body:** Length 39–48 mm, width 7.0–8.5 mm. Ground color gray. Dorsal prothoracic scoli (T1) elongated; shaft black with black and light yellow to cream colored spines. Dorsal metathoracic scoli similar to dorsal T1 scoli but with light yellow to yellow-gray rosette spines at base. Dorsal abdominal and T3 scoli rosette type with yellow to yellow-gray spines and black tips. Dorsolateral, lateral, and sublateral scoli with black shaft and light yellow to white spines. Two to three incomplete light yellow to light gray lateral lines extend length of larva; the two dorsalmost may be poorly developed. Line 1 well developed, undulating, subspiracular, extending from A2 to A9, and touching base of each lateral scolus. Line 2 lightly marked, sometimes absent, in line with dorsolateral scoli on segmental area. Line 3 passes just ventral to base of dorsal scoli; interrupted by intersegmental area. Lateral surfaces gray, dorsal area dark grayish-black. Body covered

with small light yellow to cream or light gray pinacula with a short hyaline seta extending from each. Lateral intersegmental are brown to rust. Spiracles light orange. Prominent brown dot occurs between lateral and dorsolateral scoli on A1 and A7. Ventral surface light brown. Thoracic shield black. True legs and prolegs dark brown to near black.

Kendall and Peigler (1981) published a partial description of a mature *grotei* larva but did not give the source of their material. Comparison of their larval description with larvae from Burnet Co. indicates a number of differences. Larvae from Burnet Co. have a shiny black head; reddish brown intersegmental area; scoli of three different configurations and size; and brownish orange spiracles. Kendall and Peigler described *grotei* larvae as having a rusty brown head with mottled black patches; maroon intersegmental area; almost equally developed scoli; cream colored spiracles; and concluded they were most similar to larvae of *H. burnsi* (Watson). The larval description of *burnsi* by Comstock (1937), together with my observations suggest there is little similarity between these two species. In coloration and morphology, *groeti* larvae from Burnet Co., Texas are most similar to *diana* and *diana*-like larvae from central Arizona.

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NATURAL HISTORY AND ECOLOGICAL CHEMISTRY OF THE NEOTROPICAL BUTTERFLY *PAPILIO ANCHISIADES* (PAPILIONIDAE)

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ABSTRACT. The life cycle, behavior, and chemical ecology of the neotropical butterfly *Papilio anchisiades idaeus* Fabricius (Papilioninae) were studied, using larvae from a single cluster of eggs obtained in NE Costa Rica. The butterfly places large clusters of eggs on the ventral surface of older (bluish green) leaves of *Citrus*. The larvae are cryptically colored and exhibit communal resting, molting, and nocturnal feeding behavior. Fourth and fifth instars perch on branches and trunk of the host plant. Larvae are parasitized by the braconid wasp *Meteorus* sp., and the ant *Camponotus rectangularis* attacks and kills pupae located on the host plant. Paper wasps do not attack large larvae or pupae, even though their nests are often abundant in *Citrus* trees occupied by *P. anchisiades*. Pupae on substrates away from the host plant may survive ant predation. Larvae readily evert the osmeterium when provoked; a very pungent, disagreeable odor is noticeable (to humans) only in the fifth instar. The principle components of the osmeterial secretions change both qualitatively and quantitatively with the molt to the fifth instar. The major constituents of the secretions of third and fourth instars are sesquiterpenes including "a-bergamotene", a-acoradiene, "a-himachalene", and isomers of farnesene; the main secretion of the fifth instar is dominated by isobutyric acid and 2-methylbutyric acid with sesquiterpenes, aliphatic hydrocarbons, long-chain alcohols, and carboxylic esters constituting minor constituents. The possible adaptive significance of this shift in the chemistry of the osmeterial defensive secretion is discussed.

The neotropical butterfly *Papilio anchisiades idaeus* Fabricius (Papilionidae: Papilioninae) is well known in Mexico, Central and South America (Seitz 1908, Ross 1964a, b). It is a large tailless swallowtail with velvety-black wings bearing white patches dorsally on the forewings, and deep red to lavender blotches dorsally on the hindwings. This butterfly is commonly seen around clumps or groves of *Citrus* trees (Rutaceae), the host plant of the caterpillars (Stoll 1781, Caracciolo 1981, Dewitz 1878, Moss 1919). The life cycle and early stages have been incompletely described (Caracciolo 1891, Dewitz 1878, Ehrlich & Ehrlich 1961, Jones 1881, Moss 1919, Oliveira 1977, Ross 1964a, Stoll 1781). In this paper we describe and illustrate the early stages, and present new information on the behavior of immature stages, on parasitism, predation, and egg placement. In addition, we analyzed osmeterial secretions of third, fourth and fifth instar larvae to compare

the chemistry of these defensive secretions with those of other species of *Papilio*. Since recent investigations demonstrated both qualitative and quantitative changes in the secretions between *Papilio* fourth and fifth instars of other species (Seligman & Doy 1972, Burger et al. 1978, Honda 1980a, b, 1981), we wondered if this was also the case for *P. anchisiades*.

MATERIALS AND METHODS

A cluster of 53 eggs was obtained by observing one female *P. anchisiades* ovipositing on a 4-m high lemon (*Citrus*) tree at the edge of a grassy cattle pasture at "Finca La Tirimbina" at 1300 h on 4 March 1982 in NE Costa Rica. This locality is about 10 km E of La Virgen (10°23′N, 84°07′W, 220 m elev.), Heredia Province, and well within the Premontane Tropical Wet Forest region (Holdridge 1967). The eggs were collected by cutting the branch with the leaf bearing them, and placing the cutting in a clean, air-tight, clear plastic bag. The larvae were reared following previously established methods (Young 1972), which included daily observations and periodic changing of leaves and removal of frass and other debris. The duration of each life stage was measured, and feeding and resting behavior noted. The culture of first instars was transported to Milwaukee, Wisconsin, where the rearing continued until adult emergence. During the Wisconsin rearing period, the larvae were fed leaves from a *Citrus* tree in the greenhouse at the Milwaukee Public Museum.

The rearing period extended from 4 March through 23 April 1982, and during this time osmeterial secretions were collected from all available larvae by instar. These secretions were collected in the standard way: each larva was gently pinched with fine forceps, and the everted osmeterium quickly wiped with a small square of filter paper and dropped immediately into a vial of methylene chloride. Several such "milkings" were done within an instar between 1400–1500 h, and samples were thus obtained for the third through fifth instars. Milkings from different larvae were pooled at each sampling date as follows: 24 third instars milked 1–2 April; 22 fourth instars milked 5–9 April; 22 fifth instars milked 13–19 April. The apparency of odor associated with everted osmeteria was also noted.

Chemical Analyses

Gas chromatography-mass spectrometry subdivides complex compounds into molecular weight fractions. It was done using 15 m × 0.3 mm I.D. OV-17 or SE-30 fused quartz capillary columns (J. and W. Scientific Co., Rancho Cordova, CA) in an LKB 2091 spectrometer, with a splitless injector system (J. and W. Scientific Co.). Confirmation

of the low boiling esters was accomplished on an LKB 900 spectrometer using a 2 m × 2.5 mm I.D. 10% SP-1000 packed column. Synthetic octadecyl and eicosanyl esters were chromatographed on a 2 m × 2.5 mm I.D. 1% OV-17 packed column. Both spectrometers were maintained during scanning at 70 ev, at a source temperature of 270°, and at 270 amp ionizing current.

Synthesis of Eicosanyl Esters of Valeric and Isovaleric Acids

These compounds were prepared for use as standards by combining an excess (1 g) of the corresponding acid chlorides with 1 g of eicosanol in 8 ml of pyridine. After 1 h the mixtures were poured into water and extracted into ether, washed with dilute sodium bicarbonate, and the ether evaporated. The oils were then chromatographed directly providing only one peak on a 1% SE-54 packed column.

Eicosyl valerate. Retention times, the result of component molecular weights and their percent representation in samples at a specified temperature, characterized specific complex compounds with mass spectrometry. Retention temperature 270°, MS: m/z (rel. intensity) 382(0.9 m+.), 353(0.4), 367(0.060), 340(0.4), 325(2), 280(8), 195(1), 181(1), 167(2), 158(1), 153(2), 139(4), 125(7), 111(14), 103(100, valeric acid + H), 102(17), 97(24), 85(22), 83(23), 82(10), 71(13), 70(9), 69(14), 57(21), 56(7), 43(6).

Eicosyl isovalerate. Retention temperature 265°, MS: m/z (rel. intensity) 382(0.8, m+.), 367(0.4), 340(0.2), 325(1.5), 280(7), 252(3), 195(1), 181(1), 167(2), 158(1), 153(3), 139(4), 125(6), 111(10), 103(100, valeric acid + H), 97(15), 85(19), 83(14), 71(7), 70(5), 69(9), 57(11), 43(4).

Preparation of methyl esters of osmeterial extract. Diazomethane in ether prepared from N-nitro-N-nitrosomethylguanidine (Aldrich Chemical Co., Milwaukee, WI) was added to 20 μl portions of the extract in methylene chloride until a yellow color persisted. Aliquots of this solution were directly injected.

RESULTS

Description of Early Stages

Eggs (Fig. 1) spherical, sculptured, about 2 mm diam, with lateral pair of ridges fusing into bilobed knob; honey-colored; not changing in color before hatching; duration of stage: seven days.

First instar cylindrical with fine down and slightly bulbous head; initially about 6 mm long; cuticle translucent amber, darkening to "dirty" greenish brown following first feeding on plant tissues; lateral body profile tapered; no tubercles and no discernible markings on cuticle; duration of stadium: seven days.
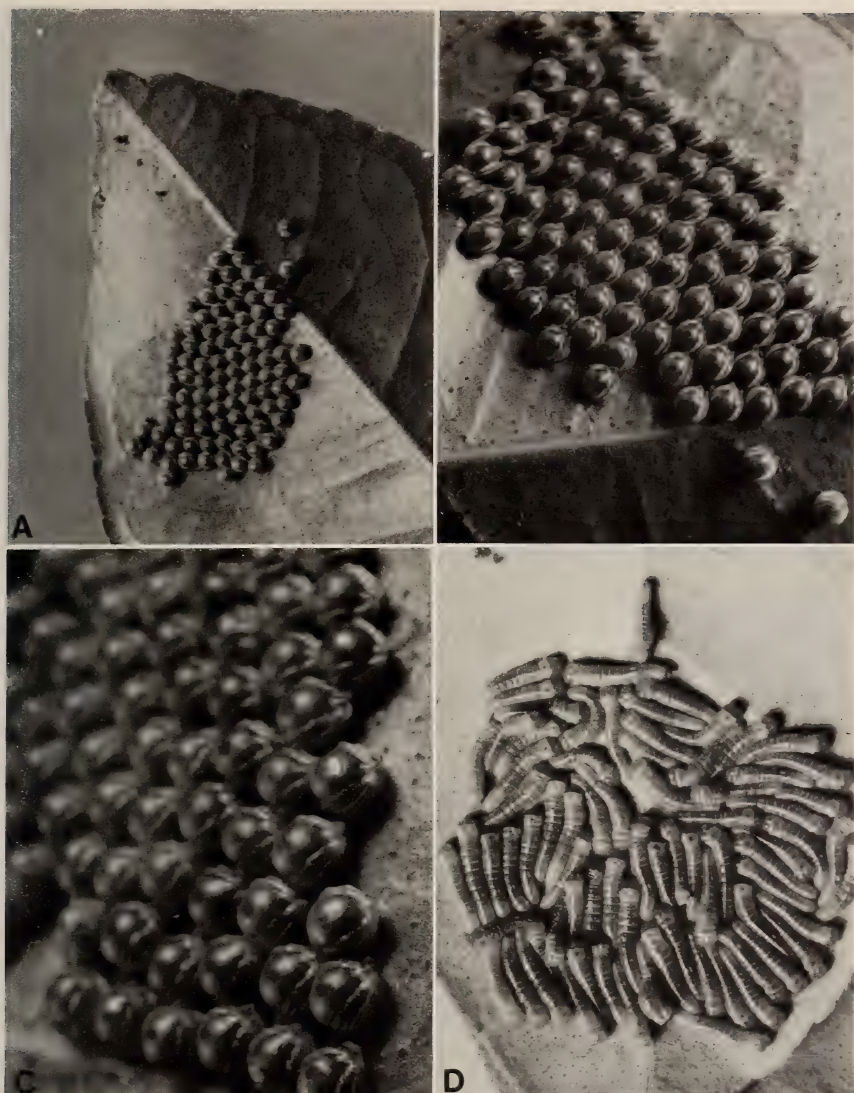
FIG. 1. *Papilio anchisiades*. (A) position of egg cluster on *Citrus* leaf (ventral surface); (B) orientation of individual eggs in cluster; (C) surface sculpturing of individual eggs; (D) second instars.

Second instar (Fig. 1) similar to first but with larger head relative to trunk; more delineation of trunk segments; first three segments and last four dull orange, middle segments greenish; head glossy orange; attained body length of 10–13 mm in seven to nine days.

Third instar (Fig. 2) strikingly different from previous instars; swelled

FIG. 2. *Papilio anchisiades.* (A) third instars immediately following molt; (B) fourth instars several days after molting; (C) fifth instar, lateral aspects; (D) aggregative behavior of fifth instars.

thoracic region; coloration a variegated brown and white cuticle with "oily" appearance; head brownish orange and glossy; head hidden and overshadowed by anterior trunk region; attained a length of 20–23 mm in eight days.

Fourth instar (Fig. 2) similar to third but with decrease in thoracic swelling; more pronounced mottling of rich brown and white blotches on trunk; both third and fourth instars with tubercles further described in Oliveira (1977); attained length of 32–36 mm in ten days.

Fifth instar (Fig. 2) with trunk cuticle "lacework" pattern of chocolate-brown background with network of lines and blotches of white; cuticle "warty" due to small tubercles and foldings (further described in Oliveira 1977); prolegs white with brown speckling; head brownish and smaller than anterior trunk; dorsally trunk cuticle bears a series of diamondlike velvety-brown blotches; attained length of 59–62 mm in 20 days. Total larval period: 45 days.

All instars with deep-orange osmeteria, short and stubby in first three instars, long and filamentous in last two. Osmeterium of fifth instar 9–10 mm long. The prepupa (Fig. 3) contracted in body length and darkened in coloration before the final ecdysis.

Pupa (Fig. 3) 37–39 mm long and 21–23 mm at greatest width; resembles broken twig; color pattern a variable mosaic of brown, gray, green, and white, but usually with large, "lichenlike" blotch on posterior two-thirds of wing pads extending posteriorly into dorsal area of abdomen; spiracle openings marked in black; duration of stage: 18–22 days. Overall egg-to-adult time: 70–74 days.

Adults eclosed rapidly, and wings were fully expanded (Fig. 3) within 25 min, and usually between 0800–0900 h. Sex ratio of 25 pupae: 10 females and 15 males.

Behavior of Stages

Eggs placed in tight rows on the ventral surface of mature *Citrus* leaf (Fig. 1); even though "young" or "fresh" (greenish-yellow) leaves available, eggs were placed on older leaf, near the distal end of the branch; butterfly clung to edge of leaf and curled abdomen under while ovipositing for 1 h. When frightened away, it did not return to resume egg laying on the same or several subsequent days. Other observations in Costa Rica indicate that this species oviposits on both mature (greenish-blue) leaves and yellowish-green fresh leaves of *Citrus* in both wet and dry forest regions. All eggs in the cluster touched one another and hatched synchronously taking about 4 h for all larvae to vacate egg shells. Egg shells were immediately devoured by larvae, and larvae remained as one group in the first two instars (Fig. 1). First instars occupied the same leaf as the eggs, and started feeding at the edge of the leaf (Fig. 4). Feeding throughout all instars was synchronous and nocturnal. Breakup into two or more subgroups began in the third instar and continued through the fifth (Fig. 2). Fourth instars

FIG. 3. *Papilio anchisiades*. (A) prepupa; (B) pupa; (C) aggregation of pupae; (D) freshly eclosed adult.

stayed in small groups on the branch rather than on leaves like previous instars.

In field observations fourth and fifth instars aggregated on the trunk of the host, and pupation occurred on the trunk, on nearby buildings or other substrates near the host.
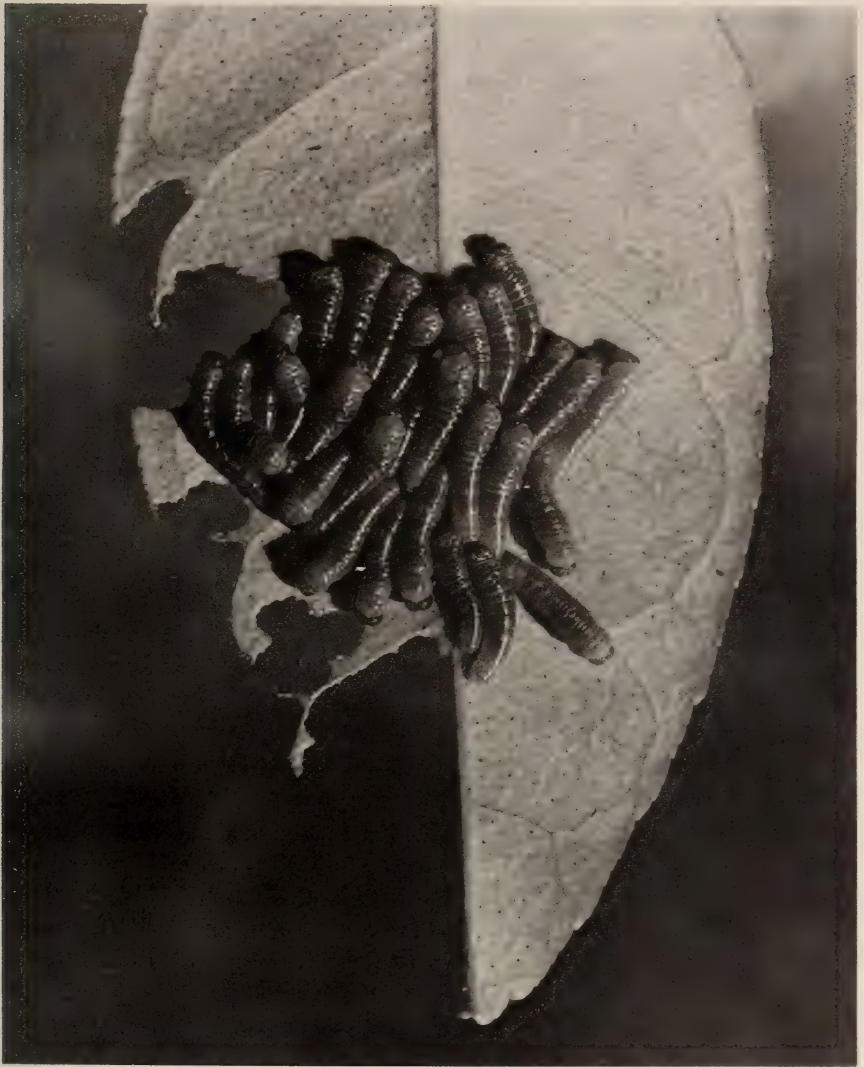
FIG. 4. *Papilio anchisiades.* Feeding pattern of young larvae on a leaf of *Citrus.*

Larvae of all five instars evert the osmeterium when prodded with forceps, but response is much quicker in the first three instars than in the last two. Eversion of the osmeteria in the first three instars was unaccompanied by odor at close range. A strong, disagreeable odor, best described as "sweaty socks," was apparent when the osmeteria of the last two instars were everted. Growth rates of larvae within a group were mostly similar, and molting was synchronous. Molting required

one to two days. However one to three individuals within the group were smaller, and differed by a full instar. Pupation appeared to occur in two "pulses," with larger larvae (presumably females) being the last to pupate.

In field observations, more than one cohort of larval *P. anchisiades* occurred in a single *Citrus* tree, often in trees with nests of paper wasps (*Polistes* and various polybiines). In a *Citrus* tree in a pasture at Palo Verde, Guanacaste Province, Costa Rica, studied between 9–11 November 1969, separate groups of 40–70 larvae were found, and each group contained 3–8 smaller larvae. Most larvae were fifth instar, and the smaller ones second and third instars. A total of nine pupae were scattered on branches, and all were being attacked by the ant *Camponotus rectangularis* Emery. An additional 25 pupae, without ants, were found on a nearby weather-beaten tool shed 5 m from the tree and separated from it by tall grasses. A total of 53 paper wasp nests were in the tree and another 74 nests on the shed. Individual wasps often perched near the pupae on the sides of the shed, but did not attack them. Pupae on the tree were not observed to be attacked by wasps. Successful eclosion of four adults was observed. No pupae on the shed were attacked by *C. rectangularis* during the two days of observation.

Several third instars collected in October 1969 at Naranja, Zaragoza, El Salvador, were parasitized by the braconid *Meteorus* sp. A second unnamed species of the same genus has been recorded from *P. anchisiades* in Venezuela (Paul Marsh, pers. comm.). Together, both records are new, and represent the first reports of parasitism by *Meteorus* on the Papilionidae (Paul Marsh, pers. comm.).

A major feature of larval behavior in *P. anchisiades* in both field and laboratory is the close physical contact among individuals, although laboratory individuals sometimes rested and fed solitarily.

Mass Spectral Analysis of Osmeterial Extracts

Extracts of the fifth instar (Fig. 5) showed a poorly resolved series of short-chain acids and esters, followed by traces of sesquiterpenes eluting from 142–170°, and finally (Fig. 6) a series of hexadecyl, octadecyl, and eicosanyl esters of butyric and valeric acids. The early eluting compounds were ethyl isobutyrate, methyl 2-methylbutyrate, ethyl 2-methylbutyrate, isobutyric acid, isovaleric acid and 2-methylbutyric acid, eluting in that order. Reexamination on a 10% SP-1000 packed column confirmed these assignments and revealed a trace of ethyl 3-hydroxybutyrate eluting just after ethyl 2-methylbutyrate. Also observed were traces of acetic acid and ethyl acetate. All compounds were identified by their mass spectra (Heller & Milne 1976). As found
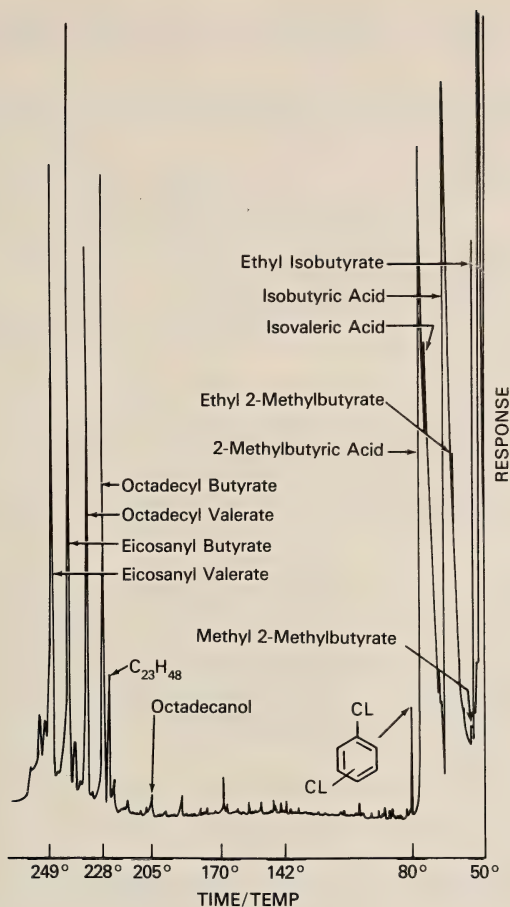
FIG. 5. Chromatographic analysis of fifth-instar osmeterial secretion in *Papilio anchisiades* (SE-30 capillary; 15 m × 0.30 mm I.D.; 10°/min.).

by Honda (1981) for other *Papilio* species, 2-methylbutyric and isobutyric acids were major components accompanied by smaller quantities of isovaleric acid. Conversion to the methyl esters allowed quantitation of these acids in the ratio 1:0.75:0.021, respectively, as determined on an SE-54 capillary column.

Expansion of the chromatographic region between 80° and 228° (Fig. 6) allowed two terpenes, a-bergamotene and E-b-farnesene (peaks 1 and 2), to be tentatively identified by comparison of their spectra with published compilations (Heller & Milne 1976). Peak 4 was tentatively identified as a-himachalene by similar comparison, while peak 9, assumed to be a sesquiterpene from its mass spectrum (Table 1), was unique to the fifth instar. The mass spectrum of peak 8 was similar

TABLE 1.   Mass spectra of sesquiterpenes identified in the osmeterial secretions of *Papilio anchisiades*. Retention temperatures (first numbers) and relative amounts ( ) refer to peaks in Fig. 7.

1. a-bergamotene: m/z 204(M+., 2), 161(3), 131(5), 119(53), 93(87), 69(53), 55(40), 43(67), 41(100)
2. A farnesene isomer: m/z 204(M+., 5), 161(6), 133(14), 119(7), 93(41), 69(100), 55(20), 43(23), 41(99)
3. B-accoradiene: m/z 204(M+., 6), 182(2), 161(6), 133(16), 120(13), 107(8), 93(50), 91(25), 81(25), 79(25), 69(100), 67(25), 57(20), 55(20), 41(90)
4. "a-himachalene": m/z 204(M+., 25), 189(7), 161(10), 147(9), 133(17), 121(25), 119(22), 93(100), 79(29), 69(21), 55(31), 43(63), 41(88)
5. A farnesene isomer (same as 2 above, but mixed with a-himachalene)
6. A farnesene isomer m/z 204(M+., 10), 161(18), 133(20), 120(18), 109(16), 93(49), 69(100), 41(79)
7. "B-selinene": m/z 204(M+., 15), 189(3), 161(3), 121(22), 119(20), 109(21), 93(100), 80(30), 69(25), 41(42)
8. Unknown: m/z 220(M+., 20), 205(5), 177(4), 163(2), 151(6), 149(4), 137(100), 135(53), 110(76), 109(51), 95(46), 82(29), 69(35), 55(40), 43(20), 41(85)
9. Unknown (only in 5th instar): m/z 204(M+., 25), 189(13), 169(31), 133(25), 121(50), 119(44), 105(52), 93(69), 91(50), 79(38), 77(31), 69(25), 55(44), 53(38), 43(81), 41(100)

but not identical to the spectrum of caryophyllene oxide reported by Honda (1981). No evidence was found for monoterpenes or the elemene, selinene or germacrenes reported by Honda (1981). Also identified in this scan were C_{14}–C_{22} saturated and unsaturated hydrocarbons as well as naphthalene, dichlorobenzene, and phthalates, all of which are regarded as artifacts.

The acid components of the hexadecyl, octadecyl, and eicosyl esters were expected to be isobutyric and either 2-methylbutyric or isovaleric acids in view of the large quantities of the corresponding free acids that were present (Fig. 5). In fact, comparison of the mass spectra of the last peak with spectra of synthesized samples of eicosyl n-valerate and eicosyl isovalerate reveals that the natural product is the former ester. Thus, the molecular ion of eicosyl isovalerate was slightly less intense relative to high mass peaks, and showed enhanced loss of methyl compared to eicosyl valerate. The other three peaks are also esters of the n-butyric and n-valeric acids by the same reasoning. Fig. 6 also shows the presence of the corresponding alcohols, octadecanol and eicosanol, easily identified by reference to library spectra.

Gas chromatograms of the third and fourth instars were nearly identical, but presented an entirely different picture (Fig. 7). Both short and long chain acids and esters were missing, and only sesquiterpenes were present. As in extracts from the fifth instar, only a-bergamotene, -acoradiene and three farnesene isomers were identified with confidence by comparison with reference spectra. The major component was a compound whose spectrum resembled, but was not identical
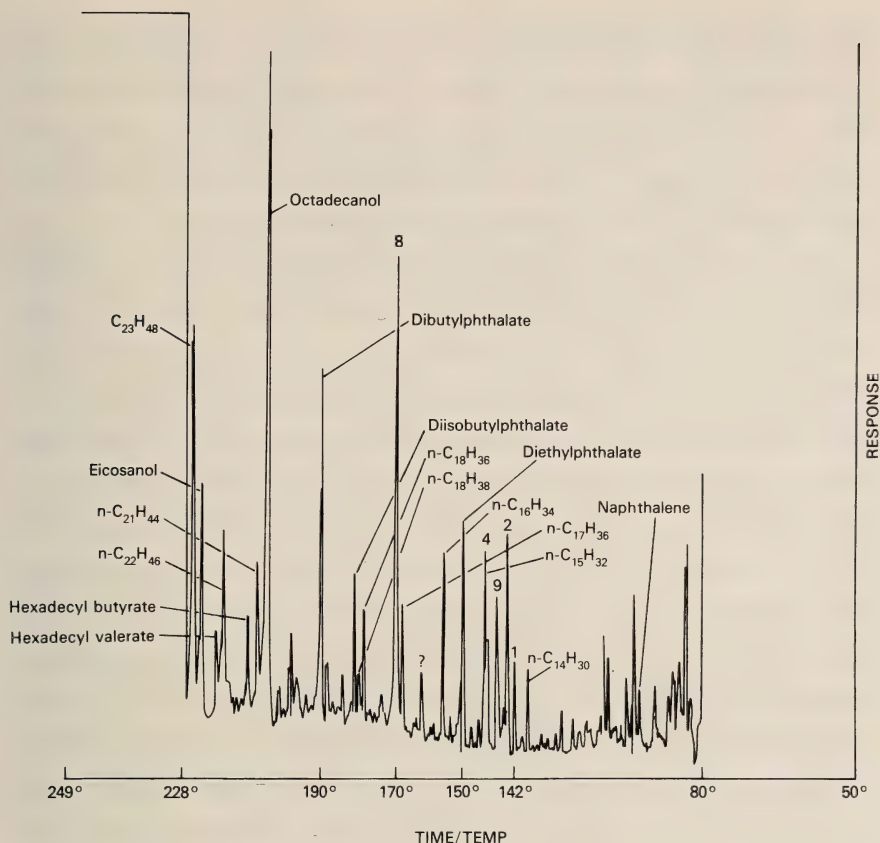
FIG. 6. Mass spectral analysis of fifth-instar osmeterial secretion in *Papilio anchisiades*, highlighting the terpene region of the spectra (SE-30 capillary; 15 m × 0.3 mm I.D.; 10°/min.).

with, caryophyllene oxide as reported by Honda (1981). Peaks 4 and 7 are very similar, and both resemble library spectra (Heller & Milne 1976) of a-himachalene or b-selinene, but neither corresponds to the b-selinene spectrum reported by Honda (1981). Mass spectra of sesquiterpenes are shown in Table 1.

DISCUSSION

Papilio anchisiades, along with *P. cresphontes* and *P. thoas*, and a few others, exploits various Rutaceae as larval food plants (Brower 1958). It differs from other rutaceous-feeding *Papilio* species by its unique larval aggregative habits, a result of cluster egg placement on the larval host plants. The rutaceous-feeding habit is shared world-

wide by several species of *Papilio* (Munroe 1960), an association perhaps mediated by the rich profiles of specific alkaloids so characteristic of this plant group (Hegnauer 1963). We propose that the widespread abundance of *P. anchisiades* from southern Brazil to Mexico and even southern Texas (Ehrlich & Ehrlich 1961), is in part due to the broad distribution of *Citrus* as an exotic rutaceous host plant coupled with the distribution of other Rutaceae with forest habitats.

Larval host-plant selection in butterflies usually involves a highly structured sequence of visual and olfactory responses (Crane 1955, Swihart & Swihart 1970, Ilse 1937). Vaidya (1969) studied the color preferences of ovipositing *P. demoleus* L. on *Citrus* in laboratory studies, and concluded that both color and scent are required for proper egg placement and noted that butterflies preferred blue-green hues of leaves over yellow-green hues. Within the Rutaceae, differences among genera and species for certain substances in the leaves determine patterns of host specificity in egg-placement behavior among different papilionids (Ichinose et al. 1981). Age-specific differences in odor and color in *Citrus* and other Rutaceae may determine patterns of egg placement in *P. anchisiades* in nature, and the field data for this species in Costa Rica supports a partial preference concept for the older, more bluish-green leaves of host plants. Depending on annual phenological patterns of flushing, such egg-placement substrates may vary in abundance at a locality and influence the abundance of the butterfly population, or result in oviposition on more yellowish green leaves. In a highly seasonal lowland area such as Guanacaste, such effects might be even more pronounced than in less seasonal Atlantic zone habitats in Costa Rica and elsewhere in southern Central America. Ross (1964b) noted that *P. thoas autocles* Rothschild & Jordan frequently oviposits on fresh leaves of the larval host plants, including *Piper* spp. (Piperaceae) and *Citrus* in Mexico. *Papilio aristodemus ponceanus* oviposits on young shoots of *Zanthoxylum fagara* (Rutaceae), "Wild Lime," and first instars readily devour the young leaves without difficulty (Rutkowski 1971). Tough, thick leaves of Rutaceae used by *Papilio* species may retard normal growth and development of caterpillars (Watanabe 1982), thereby selecting for egg placement on young, tender leaves.

Several studies reveal that the attraction of parasitoids to their phytophagous hosts is often mediated by the aromatic substances emitted by the host plant (Herrebout 1969, Read et al. 1970). We suspect that *Papilio* species associated with the highly aromatic Rutaceae are subject to such parasitism, and several larvae within an aggregate of *P. anchisiades* can be killed by the braconid *Meteorus* sp. Such interactions may extend to predatory arthropods such as the ant *C. rectangularis* associated with *Citrus* in lowland Guanacaste, even though

predation by paper wasps under the same conditions may be minimal or nonexistent.

The size of larval groups of *P. anchisiades* in *Citrus* varies, and the group observed in the present study might have been small since the ovipositing butterfly was frightened away. The larvae have been noted to defoliate a tree (Caracciolo 1891), and very large groups of larvae have been found on individual trees (Moss 1919). Pupae are often found on various substrates away from the host tree (Moss 1919), and the present study suggests that mortality from at least one ant species might be less for pupae off the host tree than for those remaining on it.

Although the disagreeable odor from the osmeteria of the older larvae is well known (Stoll 1781, Carracciolo 1891, Moss 1919), the functional role of the secretion remains unknown, although the components are defensive against ants (Honda 1983). The precise egg-placement behavior of *P. anchisiades* suggests that the species is a specialist on Rutaceae, a condition that further suggests coevolved associations with parasitoids and predators that cue into the aromatic properties of *Citrus* and other genera within the family. The cryptic appearance and behavior of larvae of all instars, and the cryptic appearance of the pupa, suggest that this species is palatable to visually foraging predators such as lizards and birds (Brower & Brower 1964). When this first-line defense is penetrated by an attacker, the odor defense associated with the osmeterium might be used to thwart attack (Eisner & Meinwald 1965, Honda 1983). All rutaceous-feeding *Papilio* species appear to have cryptic coloration and habits (Munroe 1960).

We suggest that aggregative behavior in the larval stages of *P. anchisiades* enhances visual crypsis to some predators such as birds and lizards. The combined aggregate of several fifth instars on the bark of the host tree creates the image of a mottled blotch of false lichens and bark on the trunk. Similarly, the tightly packed clusters of younger larvae on the ventral surfaces of *Citrus* leaves resemble dead or dying plant tissue destroyed by a pathogenic microorganism. A large aggregation of fifth instars positioned at the junction between the trunk and main branches of a *Citrus* tree in Trinidad resembled a "clot of wet feces" to both L. P. Brower and P. M. Shepard (L. P. Brower, pers. comm.). Aggregative behavior of the larvae, however, may not deter predation by birds. On 28 July 1986 one of us (A.M.Y.) observed an unidentified jay-size bird pluck off a *Citrus* leaf bearing 50 young third-instar *P. anchisiades* (at 0530 h) at "Finca La Lola" in Costa Rica. The bird then devoured all the larvae in a few seconds.

The osmeterial secretions from third and fourth instars of *P. anchisiades* are similar to those of other *Papilio* species in being domi-
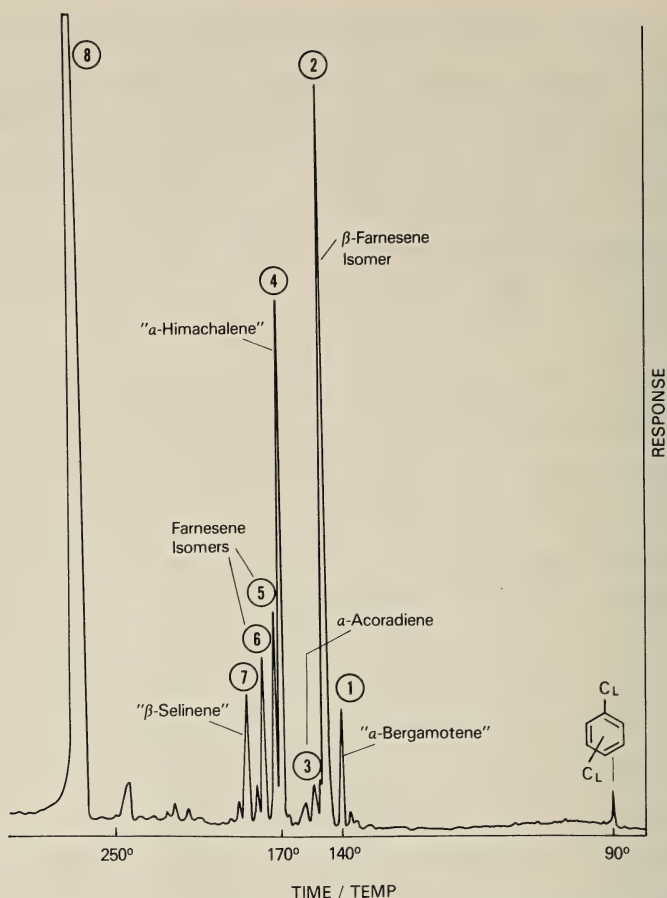
FIG. 7.   Mass spectral analysis of fourth-instar osmeterial secretion in *Papilio anchisiades*, highlighting sesquiterpene region of the spectra.

nated by terpenes. Burger et al. (1978) and Honda (1980a, b, 1981) reported that the secretions of earlier instars of several *Papilio* species are made up of mono- and sesquiterpenes. While we did not detect monoterpenes in the secretions of *P. anchisiades*, at least seven sesquiterpenes fortify the osmeterial exudate (Fig. 7). Honda (1981) previously identified sesquiterpenes in the osmeterial secretions of five species of *Papilio*, but several of those produced by *P. anchisiades* appear to be different from those produced by the Japanese species.

Earlier investigations established that the osmeterial secretions of a variety of *Papilio*, *Baronia*, and *Eurytides* species were dominated by isobutyric and 2-methylbutyric acids (Eisner & Meinwald 1965, Crossley & Waterhouse 1969, Eisner et al. 1970, Burger et al. 1978, Lopez & Quesnel 1970). However, it was subsequently demonstrated that this

acidic duet is characteristic of the osmeterial secretions of the fifth instar. In contrast, the secretions of earlier instars of several *Papilio* species lack the short-chain acids produced by fifth instars, and a variety of terpenes are produced by younger larvae (Burger et al. 1978, Honda 1980a, b, 1981).

The osmeterial secretion of the fifth instar of *P. anchisiades* contains isobutyric and 2-methylbutyric acids, but, in addition, isovaleric acid, a compound detected as a minor osmeterial constituent in two other *Papilio* species (Honda 1981). Although isobutyric and 2-methylbutyric acids have been encountered as the acidic moieties of short-chain esters in the osmeterial secretions of *P. anchisiades* and other species (Burger 1978, Honda 1981), long-chain esters containing butyric and valeric acids (Fig. 5) have not been reported previously from papilionid osmeterial secretions. Thus, fifth-instar larvae of *P. anchisiades* are distinctive in producing osmeterial secretions containing esters such as hexadecyl valerate (Fig. 6) and octadecyl butyrate (Fig. 5). It is not clear why the dominant free acids in the secretion—isobutyric and 2-methylbutyric—have not been utilized as the acid moieties of these long-chain esters.

Sesquiterpenes in the osmeterial secretion of the fifth instar is unusual, since this class of compounds has been identified in the secretions of earlier instar *Papilio* (Burger et al. 1978, Honda 1980a, b, 1981). However, one sesquiterpene has been identified in the secretion of *P. protenor* (Honda 1980), and three in that of *P. memnon* (Honda 1981). *Papilio anchisiades* is unusual in having almost as many sesquiterpenes (five) in the secretion of the fifth instar as in that of earlier instars (seven).

The secretions of the last instar of *P. anchisiades* differs from those of any *Papilio* species similarly analyzed in containing aliphatic hydrocarbons and long-chain alcohols (Fig. 7). Nine aliphatic hydrocarbons are present, and these are accompanied by C_{18} and C_{21} alcohols. With the presence of esters such as hexadecyl valerate, the distinctiveness of this osmeterial secretion is further evident.

Previous investigators demonstrated that the secretions of younger larvae were qualitatively richer than those of fifth instars (Burger et al. 1978, Honda 1980a, b, 1981); the opposite is true for the secretions of earlier and fifth instars of *P. anchisiades*. Whereas the third and fourth instar secretions contain seven sesquiterpenes (Fig. 7), the fifth instar secretion contains more than 30 compounds (Figs. 5, 6) including acids, hydrocarbons, esters, alcohols, and sesquiterpenes. Qualitatively, the fifth-instar secretion of *P. anchisiades* exceeds that known for any instars of any *Papilio* species.

If it is assumed that the chemical (osmeterial) defenses of earlier-instar *Papilio* evolved as deterrents against predators different than

encountered by the fifth instar, then the differences in the chemistry of these instars is explicable. There is little specific evidence on what organisms constitute enemies for larvae of *P. anchisiades* of any instar. Whatever the selection pressures were for producing the fifth-instar exudate, they have resulted in the most diverse osmeterial secretion encountered in the genus *Papilio*.

The greater heterogeneity and complexity of the osmeterial secretion of fifth instars in *P. anchisiades* suggests that the system becomes most functional in this instar. The pungent odor emitted in the fifth instar results from isobutyric and 2-methylbutyric acids, which are lacking in the earlier instars. The occurrence of some components (sesquiterpenes) of earlier-instar osmeterial secretions in the fifth instar indicates that the biochemical pathways underlying the synthesis of these substances are not completely turned off in the fifth instar. Both qualitative and quantitative changes figure in the regulation of secretion in the fifth instar of *P. anchisiades*.

Our results are largely due to the application of capillary-column gas chromatography, which enabled detecting of minute amounts of specific components in the fifth instar, substances that might have been overlooked otherwise.

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GENERAL NOTE

SATURNIA WALTERORUM (SATURNIIDAE) IN MEXICO: A NEW NATIONAL RECORD

Until now *Saturnia walterorum* (Hogue & Johnson) had not been taken in Mexico. It had been known to occur only in San Diego, Los Angeles, and Orange counties of California. A previous reference to specimens captured in San Luis Obispo Co. (Tilden 1945, Pan-Pac. Entomol. 21:32–33) is in error, as the cited specimens were examined by Tuskes and Collins (1981, J. Lepid. Soc. 35:1–21) and found not to be typical *walterorum*.

Both male and female are diurnal, and are not attracted to light. The seasonal flight period appears restricted to a few of the warmest days between late February and early June (Tuskes 1974, J. Lepid. Soc. 28:172–174). The insect is not abundant, and is easily overlooked.

Our experience with this species in coastal San Diego Co. suggests the peak daily flight period for males is mid-morning, diminishing greatly before noon.

On 1 April 1985 at 1130 h, we placed two newly emerged captive-reared females of this species in a screen cage among chaparral near Ensenada, Baja California, Mexico, about 100 km south of the United States border. The small amount of natural vegetation at this site was similar to that of areas near San Diego, California, and included *Rhus laurina* (Nuttall) and species of *Ceanothus*, *Rhamnus* and *Adenostoma*. *Rhus laurina* appears to us to be the preferred food plant of *Saturnia walterorum* in the coastal areas of its range.

At 1140 h a single male was attracted to the calling females and was captured. No additional males had appeared by 1300 h, at which time we left the area.

The captured specimen was placed in the San Diego Natural History Museum, San Diego, California.

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PYRGUS COMMUNIS AND *P. ALBESCENS* (HESPERIIDAE) IN NEVADA

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ABSTRACT. Based on more than 500 male genitalia, the *Pyrgus communis* phenotype replaces the *P. albescens* phenotype latitudinally and elevationally in Nevada. Intermediates are known where their distributions meet and overlap.

The status of *Pyrgus communis* (Grote) and *Pyrgus albescens* Plötz (Hesperiidae: Pyrginae) has been in question up to the present. They have been treated as separate species, as subspecies, or neither (Tilden 1965). Even the most recent regional and taxonomic treatments vary. They were considered subspecies of *P. communis* by Stanford (*in* Ferris & Brown 1981) but as full species by Miller and Brown (1981). The two taxa are often segregated by ecology and geography but there are areas of sympatry or near sympatry in southwestern United States and adjacent Mexico. In some latter areas, intermediates are known (Tilden 1965). In others, they are said to occur in close proximity, but no mention is made of intermediates (Ferris 1976, Stanford *in* Ferris & Brown 1981, Holland 1984); some workers have never seen an intermediate (Ferris, H. A. Freeman, pers. comm.). The present paper summarizes their status and distribution in Nevada.

More than 500 male adults from Nevada in the Nevada State Museum and in the author's collection were examined. The left valva of each was classified into one of three configurations, the variations of which are indicated in Fig. 1. These were assigned to *P. albescens*, *P. communis*, and intermediate, and their distributions were mapped.

The valvae of individuals assigned to nominate *P. communis* have a long and recurved dorsal process terminating in two sharply pointed prongs (Fig. 1). The lengths of the dorsal process and the prongs vary. On some individuals, one of the prongs is shorter than the other; on most they are equal. The valvae of individuals assigned to *P. albescens* have no dorsal process but usually have a single, short prong anterior to the tip (Fig. 1). Intermediates show various degrees of development in the dorsal process and the double prongs (Fig. 1). There was no difference in wing pattern between the genitalic phenotypes; their seasonal variation is likewise identical.

Individuals of the *P. communis* phenotype occur throughout Nevada (Fig. 2); those of the *P. albescens* and intermediate phenotypes occur in southern Nevada except for one *P. albescens* from Carson City (Fig. 2). At most stations where *P. albescens* were taken, inter-
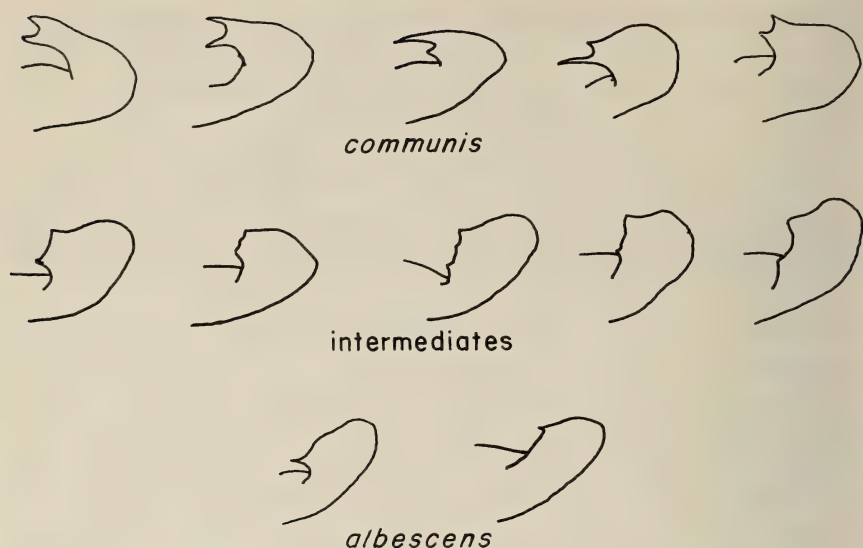
FIG. 1. Variation in the left valvae of *Pyrgus communis* in Nevada.

mediates and *P. communis* were taken also. Individuals with intermediate valvae occur only within the range of *P. albescens*. There is no strict ecological or elevational segregation in southern Nevada, but phenotype proportions do vary. The *P. albescens* phenotype dominates at lower elevations and latitudes. Intermediates and *P. communis* become more prominent with increase in elevation and latitude (Table 1, Fig. 2). In the Newberry Mountains, Las Vegas Valley, and the lower slopes of the Spring Mountains, *P. albescens* accounts for more than 60% of the individuals, and *P. communis* for less than 6%. At moderate elevations of the Spring Mountains, there is an increase in the *P. communis* phenotype and at the higher elevations and in Moapa Valley, intermediates predominate.

The Nevada distribution is compatible with that previously noted

TABLE 1. Proportion of *P. albescens, P. communis* and intermediate phenotypes from different locations in southern Nevada.

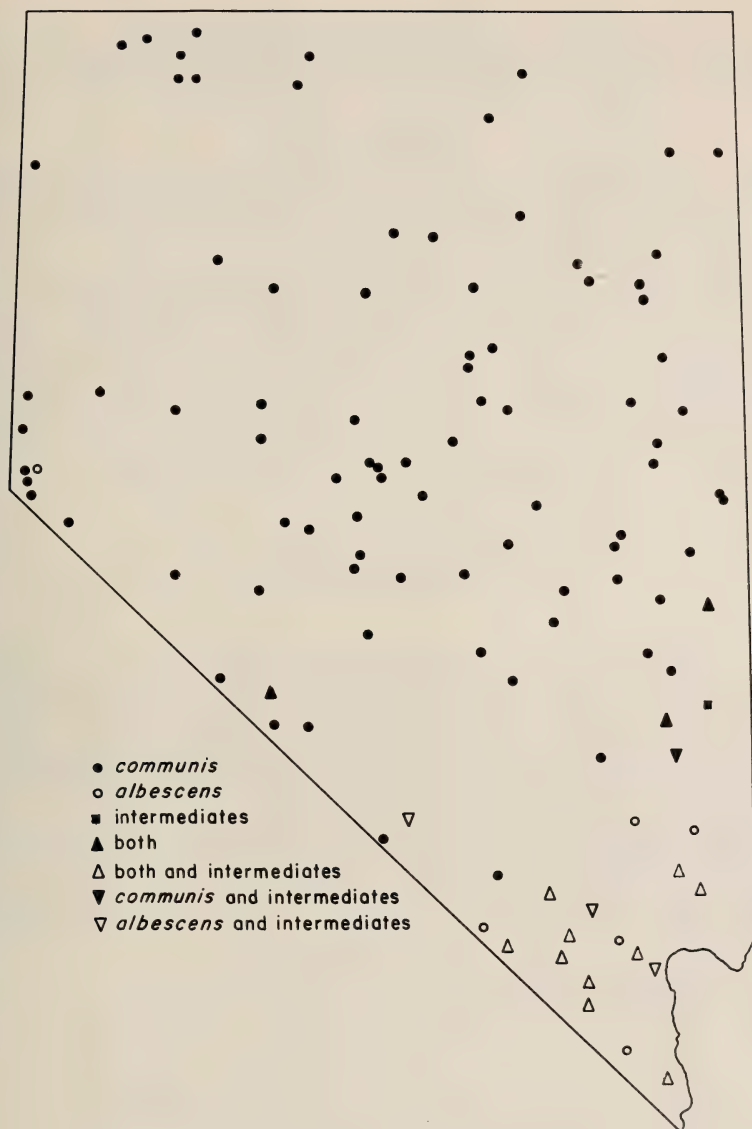| Location	*P. albescens*	Intermediate	*P. communis*	N
Newberry Mountains (<1,200 m)	60	36	4	25
Las Vegas Valley (600–900 m)	62	33	5	21
Low slopes, Spring Mts. (<1,500 m)	65	29	6	17
Mid elevations, Spring Mts. (1,500–2,100 m)	57	24	19	84
High elevations, Spring Mts. (>2,100 m)	20	60	20	15
Moapa Valley	34	48	18	91

FIG. 2. Distribution of *Pyrgus communis* in Nevada.

(Tilden 1965) for *Pyrgus communis*; the latter is a more northern and higher elevation phenotype, *P. albescens*, a lower-elevation and more southerly phenotype. Intermediacy, at least in southern Nevada, is greater than previously reported. This indicates that the two phenotypes are closely related, and are probably no more than allopatric subspecies of *Pyrgus communis*.

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ANNOUNCEMENT

INAUGURATION OF MANUSCRIPT DATING IN THE *JOURNAL*

Received and accepted dates will appear at the end of all research reports published in the *Journal* starting with submissions received in 1986. Such dating is practiced by many scholarly journals. It has at least three purposes. First, it encourages editors, reviewers, and authors to speed manuscript processing. Second, it tells prospective contributors how long manuscript processing might take. Third, it enables more accurate dating of ideas should issues of history or priority arise.

To better serve these purposes, new received dates may be assigned to some revised manuscripts. Examples are those received more than two years after the editor requests them, and those with excessively broadened scopes.

Received and accepted dates should make the *Journal* more useful to readers and authors alike.

WILLIAM E. MILLER, Editor

FIRST REPORTED MALES, SPECIES STATUS, AND AFFINITIES OF *EPARGYREUS SPANNA* EVANS (HESPERIIDAE)

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ABSTRACT. Two males of *E. spanna*, an Hispaniolan endemic formerly reported from only two females, were collected in Pedernales Province, Dominican Republic, in 1985. Male genitalia and other characters support species status of *E. spanna* but not its long-supposed affinity to *E. antaeus* Hewitson, endemic to Jamaica, and to *E. zestos* Geyer of trans-Caribbean distribution. Genitalically, *E. spanna* resembles *E. windi* Freeman of Mexico, *E. aspina* Evans of Colombia and *E. tmolis* Burmeister of western Argentina. Apparent affinities of *E. spanna* and some other recently described Antillean endemics do not support the island subspecies view of Caribbean biogeography. These taxa evidence most immediate kinship to particular mainland taxa, not most geographically proximate Antillean congeners.

Epargyreus spanna Evans (1952) has hitherto been known only from the holotype female (labelled "Santo Domingo" [Dominican Republic (DR)]) in the British Museum (Natural History), and a second female reported by Gali and Schwartz (1983) from west of Jayaco, La Vega Province, DR in the Albert Schwartz collection (Miami, Florida).

Brown and Heineman (1972) suggested that *E. spanna* might represent a subspecies of *E. antaeus* Hewitson. The latter is endemic to Jamaica, and among Antillean *Epargyreus*, shares with *E. spanna* the bright silver-white undersurface stripe on the hindwing. Riley (1975) figured both species, and Gali and Schwartz (1983), on the basis of wing character comparison, considered the two different species, pending examination of *E. spanna* males. Both Evans and Freeman (1969, 1977) emphasized the importance of male genitalic characters in differentiating *Epargyreus* taxa.

In 1985, we collected extensively in the DR and, in Pedernales Province, collected two female and two male *E. spanna*. The precise localities of these collections are: (1) a female of 30 mm forewing length (base to apex) taken between 0930 and 1200 h (EDT) on 30 June 1985 at 1,350 m altitude, Aceitillar, 12 km NW of Las Abejas, Pedernales Province, DR, on a mountain path, in mesic broad-leaf deciduous forest, in sunny weather (in David Matusik Collection [DMC]); (2) a female (not measured) taken at same location at about the same time on 1 July 1985 (in the Museo Nacional de Historiá Natural, Santo Domin-

FIG. 1.   "Designated allotype" male of *Epargyreus spanna*. Left: upper surface; right: undersurface.

go); (3) a male of 28 mm forewing length taken between 0930 and 1200 h (EDT) on 4 July 1985 at 1,250 m altitude, about 5 km NNW of the locality cited in (1) in mesic broad-leaf deciduous forest, in partly sunny weather (DMC); and (4) a male of 29 mm forewing length taken at the same location at about the same time on 3 July 1985. Both females were collected while flying about 13 cm above the ground in zigzag flight, which alternated with periods of alighting on patches of bare ground usually about 4 m apart. Both males were collected while perched on broad-leaf deciduous foliage about 2.4 m above the ground, between leaf-to-leaf flights. The flight of males between leaves was notably slower than that of the females between patches of bare ground. The dates cited above, along with that of Gali and Schwartz [17 August], indicate the flight period of *E. spanna* to be at least three weeks.

Considering the apparent rarity of *E. spanna*, and for reference purposes, we follow Smith (1983) and designate the last-cited male as "designated allotype". The specimen, marked as such, is in the collection of the American Museum of Natural History (AMNH), and is illustrated here (Fig. 1). The category "designated allotype" has no status according to the International Commission on Zoological Nomenclature Code, but is viewed as having diagnostic utility (Frizzell 1933, Gloyd 1982, Smith 1983).

Collection of the *E. spanna* male enabled examination of its genitalia (Fig. 2). Comparison of the genitalia with other *Epargyreus* taxa available to us in AMNH genitalic material of W. H. Evans and H. A.
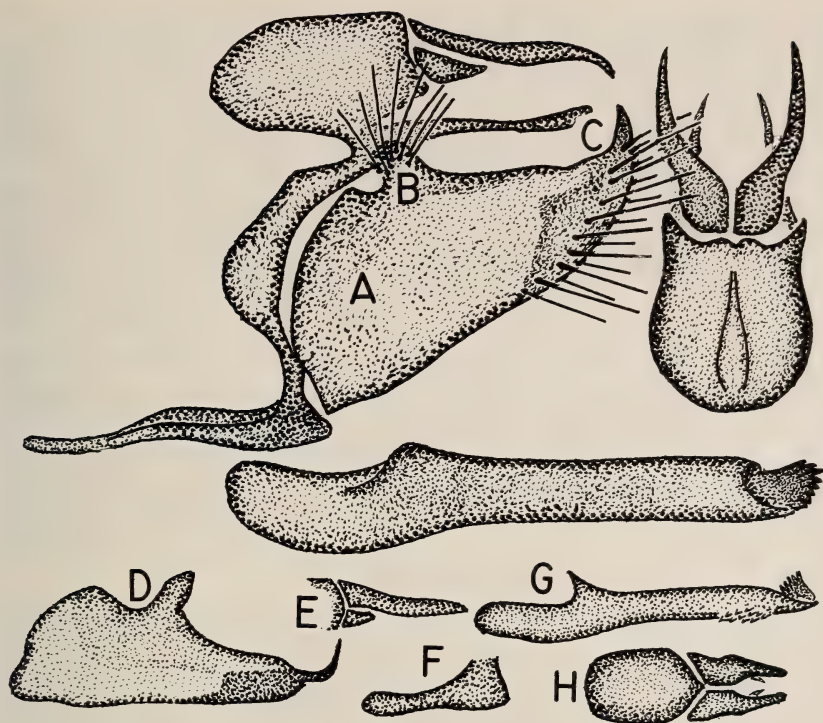
FIG. 2. Male genitalia of *Epargyreus spanna* and *E. antaeus*. Above right: Dorsal view of *E. spanna* uncus and tegumen. Above left: Lateral view of *E. spanna* genitalia with aedeagus removed. A, Broad cephalad area; B, Reduced, cephalad-located dorsal process; C, Broadly thickened terminus with wide-based terminal hook. Immediately beneath: Lateral view of *E. spanna* aedeagus. Bottom: *E. antaeus*. D, Lateral view of valve; E, Lateral view of uncus; F, Lateral view of saccus; G, Lateral view of aedeagus; H, Dorsal view of tegumen and uncus.

Freeman indicates that *E. spanna* is specifically distinct from its congeners. These taxa are *spina* Evans, *aspina* Evans, *antaeus*, *orizaba* Scudder, *exadeus* Hübner, *windi*, *cruza* Evans, *deleoni* Freeman, *spinosa* Evans, *clarus* Cramer, *brodkorbi* Freeman, *zestos*, *tenda* Evans, plus additional taxa studied from figures in Evans (1952). The genitalia do not reflect the close relation claimed for *E. spanna*, *E. antaeus* and *E. zestos* by Brown and Heineman (1972) and Riley (1975). Although *E. spanna* is similar to *E. antaeus* on the wing undersurface, the genitalia of *E. spanna* are most like *E. windi* Freeman (type locality [TL] Ajijic [Jalisco], Mexico) and also similar to *E. aspina* Evans (TL Bogotá, Colombia) and *E. tmolis* Burmeister (TL Buenos Aires, Argentina). Along with *E. spanna*, the above three taxa have on the male valvae a broad cephalad area (Fig. 2, A), a reduced and cephalad located

dorsal process (Fig. 2, B), and a broadly thickened terminus with wide-based terminal hook (Fig. 2, C). *Epargyreus zestos* and *E. antaeus* share more elongate valvae, with centrad located dorsal process, narrow terminus, and thin terminal hook (Fig. 2). *Epargyreus windi* exhibits a large, but centrally limited, silver-white patch on the hindwing under-surface, which might further suggest affinity to *E. spanna*.

The above genitalic similarities do not necessarily override the close sister species relation posited by some for *E. spanna*, *E. antaeus* and *E. zestos*. No one has done a cladistic analysis of *Epargyreus*, but the apparent affinity of genitalic and wing characters summarized above suggests that Antillean *Epargyreus* species exhibit character states rooting them as primitively in phylogenetic diagrams as their mainland congeners. The suggested genitalic affinities of *E. spanna* are remarkable because they suggest phylogenetic and zoogeographic relations contrary to the common practice of associating Antillean endemics as subspecies of various mainland or Greater Antillean taxa (Riley 1975, Clench 1965). If the latter were true, one would expect the wing character affinities for *E. spanna*, *E. antaeus*, and *E. zestos* to be closely supported by characters of the genitalia.

Johnson and Matusik (1986) noted a similar situation in the genitalic characters of a new, apparently endemic Hispaniolan *Tmolus* (Lycaenidae). This species does not resemble its most geographically proximate Antillean or mainland congener. Steven Steinhauser [Allyn Museum of Entomology] (pers. comm.) concurs regarding the genitalic characters of *Astraptes christyi* Sharpe of Hispaniola. *Astraptes christyi* has long been treated as a subspecies *A. xagua* Lucas (Riley 1975), even though it differs from that taxon in characters of the wing. Genitalic examination of *A. christyi* indicates species status and affinities not simply reducible to sympatric *E. xagua*. Schwartz and Miller (1985), in describing a new endemic Hispaniolan *Strymon*, demonstrate other affinities than might be presupposed from the most geographically proximate congener. We recently collected in Hispaniola an undescribed species of *Nesiostrymon* which cannot be regarded as *N. celida aibinito* Comstock & Huntington of Hispaniola, or of the *N. celida* Lucas complex now divided into island subspecies. The practice of placing Antillean populations of butterflies as subspecies of other, more common Antillean or mainland species seems to have resulted from certain zoogeographic assumptions. Many authors believed that Antillean butterfly distributions represent results of recent (Pleistocene and post-Pleistocene) waif dispersal (Comstock & Huntington 1943, Clench 1965). Such assumptions have been strengthened by limiting comparisons to wing patterns and interpreting differences in these as "variation" without reference to structural characters.

In zoogeography there is currently an increased appreciation of the possible correlation of late Mesozoic and Cretaceous plate tectonic splitting, and allopatric speciation of biological populations now representing various areas of endemism (Rosen 1975). This view predicts Antillean endemics may exhibit arrays of characters as primitive as any of their mainland counterparts. It is apparent that the affinities of *E. spanna* do not support the simplistic island subspecies view of Caribbean biogeography. We expect that future cladistic analyses of *Epargyreus* and other butterfly groups will suggest the early origin of many endemic Antillean taxa.

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GENERAL NOTES

EMERGENCE OF ADULT *ECTOMYELOIS MURISCUS* (DYAR) (PYRALIDAE) FROM A POD OF *THEOBROMA SIMIARUM* DONN. SMITH (STERULIACEAE) IN COSTA RICA

The pyralid moth *Ectomyelois muriscus* (Dyar), a species widely distributed in Central America, northern South America, and the West Indian archipelago, undergoes its life cycle in the pods of *Theobroma cacao* Linnaeus (Sterculiaceae) and other fruits (Heinrich 1956, American moths of the subfamily Phytcitinae, U.S. Natl. Mus. Bull. No. 207). I have been unable to locate published records of this moth species infesting pods of other *Theobroma*, a genus represented by several species in tropical America (Cuatrecasas 1964, Cacao and its allies—A taxonomic revision of the genus *Theobroma*, Contrib. U.S. Natl. Mus. 35:379–614). Given the marked differences in external texture, pubescence, and other morphological features of pod walls among *Theobroma* species, one might expect some degree of ovipositional selectivity to exist for moth species associated as larvae with pods of these neotropical tree species. Here I report the emergence of 41 adults of *Ectomyelois muriscus* from one rotted and dried pod of *Theobroma simiarum* Donn. Smith in Costa Rica, representing a new host record for the moth, and for a *Theobroma* species with mature pods differing markedly in pod-wall texture from the previously reported host, *T. cacao*.

One of 12 fallen, mature, and decaying pods of *T. simiarum* was collected beneath one of four trees of this species in the "*Theobroma* and *Herrania* garden" on the grounds of the "Centro Agronomico Tropical de Investigaciones y Ensenanza" (CATIE) at Turrialba (9°55'N, 83°41'W; about 600 m elev.), Cartago Province, Costa Rica in mid-August 1984. The 26 × 8 cm brown pod had no external insect emergence holes at the time it was collected. Subsequently the pod was kept on a desk in an office. Following an initial emergence of a few moths, I confined the pod in a plastic bag in the office. All adults were kept, and voucher specimens sent to the U.S. Dep. Agr. Systematic Entomology Laboratory (U.S. National Museum) for determination.

Between 20 October and 7 December 1984, 42 moths emerged from the pod, with an approximately 1:1 sex ratio. From one to four moths emerged on a given day during this period, but there were many days when no moths emerged. Most moths emerged before 0800 h. Several freshly-eclosed moths clung motionless to the pod for several hours, and flew only when disturbed. By the time the last moth emerged, only three exit holes were found on the external surface of the pod. Clearly, several moths used the same exit holes for emergence. Each exit hole had a 10–25 mm long silken tube externally, apparently built by larvae inside the pod wall and pushed out at the time of multiple eclosions. But eclosion behavior was not observed. Nor did I open the pod to determine where larvae were feeding, as the intact fruit was necessary for other research purposes.

The adults exhibited a staggered emergence pattern, because the emergence period lasted about six weeks. The female moth probably deposits clusters of eggs on the external surface of the sand-papery-rough pubescent pod, since adults appeared to emerge in clusters from a few exit holes. Perhaps this particular pod received three different egg batches. Assuming the observed laboratory emergence pattern was similar to that occurring in nature, a brood of *E. muriscus* emerges near the end of the Turrialba rainy season, and before the short, erratic dry season. The availability of decaying pods of *T. simiarum* varies greatly throughout the year, suggesting a changing pod supply for pod herbivores or pod saprotrophs (whichever the case may be).

Given the previously reported association of *E. muriscus* with *T. cacao* in both Central and South America, my discovery of this moth species in a pod of *T. simiarum* may not be surprising. *Theobroma simiarum* is one of two species of the genus endemic to Costa Rica. Given the broad geographical range of *Ectomyelois muriscus* in tropical America, it undoubtedly has other natural hosts, possibly species of *Theobroma* other

than *cacao* or *simiarum*. The dense, thick tomentum (pod wall external surface) may represent a suitable oviposition substrate for *Ectomyelois muriscus,* but other surface textures must also be suitable given the marked difference in this feature between *Theobroma cacao* and *T. simiarum*. Larvae of *Ectomyelois muriscus* most likely tunnel through the woody epicarp and softer mesocarp tissues of the pod. Yet they may infest pods once the latter are into advanced stages of decay, perhaps rendering pod-wall tissues more penetrable to larvae.

Near the end of the rainy season at this locality, mature pods of various species of *Theobroma* are available, in addition to those of *T. cacao,* the most abundant species due to large commercial plantations. When the dry season arrives near the end of December, dryness may trigger a large moth emergence, a pattern somewhat different than that observed in the office. The very dry conditions of the office may have mimicked the dry season for moth larvae and pupae present inside the *T. simiarum* pod, leading to a staggered emergence as conditions became increasingly dry.

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THE FEMALE OF *PAPILIO XANTHOPLEURA* GODMAN & SALVIN (PAPILIONIDAE)

Before 1985, literature concerning *Papilio xanthopleura* Godman & Salvin stated that its female occurs in two forms: a "normal" female resembling the male, and a large yellow one, form *diaphora* Staudinger (Staudinger 1891, Deut. Entomol. Z. [Iris] Lepid. 4:61–158; Rothschild & Jordan 1906, Novit. Zool. 13:412–752; Jordan 1907, *in* Seitz, Macrolepidoptera of the World, Vol. 5, Alfred Kernen Verlag, Stuttgart, 592 pp.; Munroe 1961, Can. Entomol. Suppl. 17, 51 pp.; D'Almeida 1965, Catalogo dos Papilionidae Americanos, Soc. Braz. Entomol., Sao Paulo, 366 pp.; D'Abrera, Butterflies of the Neotropical Region, Part 1, Papilionidae and Pieridae, Lansdowne Editions, East Melbourne, 172 pp.). None of the literature illustrates a *xanthopleura* female.

Johnson, Rozycki and Matusik (1985, J. N.Y. Entomol. Soc. 93:99–109), examined the type and other specimens of *diaphora,* and showed that the type and all known representatives of *diaphora* are males, and male genital and wing characters in *diaphora* indicate it is not conspecific with *xanthopleura*. As a result, *diaphora* was accorded species status, it became apparent that females of *diaphora* are presently unknown in collections, and no "normal" females of *xanthopleura* were in the following major collections: Allyn Museum of Entomology, American Museum of Natural History (AMNH), British Museum (Natural History), Carnegie Museum of Natural History, Collection of David Matusik (Skokie, Illinois), Collection Dep. de Zoologia, Universidade Federal do Paraná (Brazil), Collection of Ernesto W. Schmidt-Mumm (Bogotá, Colombia), Collection of Rick Rozycki (Chicago, Illinois), Collection Tommasso Racheli (Rome, Italy), Instituto de Zoologia Argricola Maracay (Venezuela), Museu Nacional, Rio de Janeiro (Brazil), Museo de Historia Natural "Javier Prado" (Lima, Peru), National Museum of Natural History (Smithsonian Institution), and the collection of a commercial dealer noted for his holdings in unusual Papilionidae.

Therefore, we borrowed a female of *xanthopleura* (Fig. 1A, C) from the Staudinger Collection (Zoologisches Museum der Humboldt Universität, Berlin, German Democratic Republic [ZMH]). The female resembles male *xanthopleura* on the wing undersurface but, contrary to the above literature, differs markedly from the male on the upper surface of the wings. Males of *xanthopleura* are black above except for brilliant "powder green"

FIG. 1.   *Papilio xanthopleura* and *P. diaphora*, with forewing length (base to apex) in parentheses, B–D, upper surfaces of wings, to same scale, A, undersurface, to different scale. A, *P. xanthopleura* female (67.0 mm), Iquitos, Peru, ZMH; B, *P. diaphora* type male (71.0 mm), Manicoré, Brazil, ZMH; C, *P. xanthopleura* female (of 1A); D, *P. xanthopleura* male (57.0 mm), Campana [sic], Brazil, AMNH.

in the vein interspaces of the hindwing (Fig. 1D); females are powder green over the entire upper surface of both wings (Fig. 1C). Female *xanthopleura* are larger than male *xanthopleura*, but neither exceeds the large size of male *diaphora*. As noted by Johnson, Rozycki and Matusik, the mean single forewing length (base to apex) of known *diaphora* males exceeds that of examined *xanthopleura* males by 12.3 mm and the examined *xanthopleura* female by 3.0 mm. Thus, wing character differences in the genders of these taxa vary far more than the literature has indicated.

We thank Prof. H. J. Hannemann for loan of the *diaphora* type and various *xanthopleura* specimens. Phillip Ackery, K. S. Brown, O. H. H. Mielke, L. D. Miller, John Rawlins, R. K. Robbins, Tommasso Racheli, and E. W. Schmidt-Mumm aided in surveying various collections.

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PLACEMENT AND FATE OF MONARCH BUTTERFLY PUPAE
IN NORTHERN CALIFORNIA

The placement on a substrate and the subsequent fate of *Danaus plexippus* (L.) (Danaidae) pupae were determined on a roadside strip at two sites SE of Davis, Yolo Co., California, in the Sacramento Valley from mid-July to October 1966.

The first site was 3 km south of Davis. It was a strip 4 m wide and about 400 m long containing several clumps of *Asclepias fascicularis*, other green plants, and dry grass between a paved road and a woven wire fence. The second site was similar and 6 km SSE of Davis. Both were in flat, mostly agricultural land, and near alfalfa, sugar beets, and grains. The only trees were around a dwelling and an old church and cemetery.

Each site was thoroughly searched on weekends and occasionally during the week from 14 July to 30 October 1966. Each pupa was marked with a paper tag located nearby with a serial number and date of discovery.

Vertical distributions of pupae were from ground level to 1 m. One pupa was found 4 m high on an old creosoted pole.

Choices of substrate for 409 pupae were: *A. fascicularis,* 17.7%; other green plants, 6.2%; dry grass, 47.7%; wire fence, 25.5%; and wooden fence posts, 2.9%. Only 4% of the pupae on the *A. fascicularis* were placed after 31 August. On the wire fence, 6% were placed in July, 25% were placed in August, 53% in September, and 16% in October. On dry grass, 24% were placed in August, 53% in September, and 23% in October. Pupae are rarely placed on *Asclepias* spp. in southeastern Canada (Urquhart 1960, The Monarch Butterfly, Univ. Toronto Press, 361 pp.).

Following initial observations, several categories of pupal fate were defined but only three are reported (Table 1). The latter are: discolored and dead, empty shell left after eclosion, and disappeared leaving no evidence of fate (because pupae were marked with white tags, passersby may have taken some, but predation seems more likely).

TABLE 1.   *Danaus plexippus* pupal fate by substrate, Davis, California, 1966.

Fate	Number of pupae				
	Dry grass	*Asclepias fascicularis*	Other green plants	Wire fence	Total
Died	83	25	9	21	138
Eclosed	74	32	14	35	155
Disappeared	54	18	4	23	99
Total	211	75	27	79	392

Without regard to substrate' 39.4% eclosed, 35.1% died, and 25.5% disappeared (Table 1). Of the 99 that disappeared, 55% were on dry grass, 28% on the wire fence, and 24% on green plants. The data were analyzed in a standard contingency table; $\chi^2 = 7.18$, df = 6, .500 > P > .250. The sample may be too small, but tentatively, pupae on green plants appear to be safest from predators. A higher percentage of pupae eclosed on green plants than on dry grass or the wire fence.

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ABERRANT POSTMEDIAL SPOTS IN
ICARICIA ICARIOIDES LYCEA
AND *I. ACMON* (LYCAENIDAE)

Several nearctic lycaenids tend to abnormal expression of ventral postmedial spots. This generically takes the form of some or all spots being elongated. Illustrations recently published include a multiple occurrence in *Satyrium calanus falacer* (Godart) (Wright 1981, J. Lepid. Soc. 35:158–159). Single occurrences have been shown for *Satyrium acadica acadica* (W. H. Edwards) (Leeuw 1979, J. Lepid. Soc. 33:204–205), *Glaucopsyche lygdamus couperi* Grote (Neil, 1983, J. Lepid. Soc. 37:258), *Euphilotes rita rita* (Barnes & McDunnough), *Icaricia acmon texana* Goodpasture (Holland 1980, J. Res. Lepid. 19: 88–95) and *Icaricia acmon lutzi* (dos Passos) (Cannon, J. Lepid. Soc. 39:329–330). The similarity of the two aberrant *acmon* specimens is striking, especially since the *acmon lutzi* is from Idaho and the *acmon texana* is from New Mexico.

To this list of aberrant lycaenids, I now add *Icaricia icarioides lycea* (W. H. Edwards). Figure 1 shows an aberrant, an intermediate and a typical specimen. About 5% of 100 specimens were found to have noticeably enlarged postmedial spots. The two atypical examples illustrated here represent the most extreme.

I call attention to a well illustrated and useful article on the mechanics of color pattern formation and malformation in butterflies and moths (Nijhaut 1981, Sci. Am. 245(5): 140–151). This work seems not to have received the recognition it should among lepidopterists.

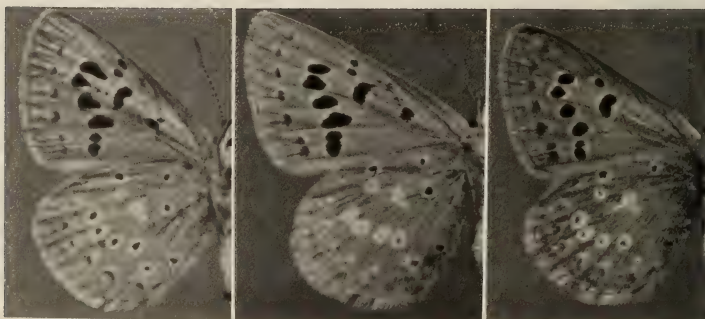RICHARD HOLLAND, *1625 Roma NE, Albuquerque, New Mexico 87106.*

FIG. 1. *Icaricia icarioides lycea* ventral surface. Left, aberrant male, Corral Tank, Canyon de Los Corrales, NE slope, Jemez Mts., Rio Arriba Co., NM, 27.V.84, 2,438 m; Middle, intermediate male, 1.6 km N of Poncha Pass, Chaffee Co., Colo., 5.VII.63, 2,743 m; Right, normal male, 20.9 km W of Española on road to Santa Clara Peak, E slope, Jemez Mts., Rio Arriba Co., NM, 18.VI.83, 2,499 m; all leg. R. Holland.

NOTES ON A COSTA RICAN "MONKEY SLUG" (LIMACODIDAE)

Little is known about the life cycles, larval food plants and other aspects of natural history of neotropical limacodids (Dyar 1924, Limacodidae, *in* Macrolepidoptera of the World, Vol. 6. American Heterocera [A. Seitz, ed.], A. Kernan Verlag, Stuttgart). Herein I describe the final instar caterpillar, some aspects of caterpillar behavior, and one larval food plant for *Phobetron hipparchia* Cramer in northeastern Costa Rica. Dyar mentions that *P. hipparchia* caterpillars feed on "different forest trees" and that this species occurs in Mexico, Panama, Ecuador, Colombia, Venezuela, Guiana, Brazil, and Argentina.

On 27 February 1985, two late-instar caterpillars of *P. hipparchia* were collected from one 6 m tall *Gliricidia sepium* (Jacq.) Steud. (Papilionoideae: Galegeae, Robiniinae) supporting vanilla vines at "Finca La Tirimbina," near La Virgen, Sarapiqui District, Heredia Province (10°23′N, 84°07′W; 220 m elev.). The tree was one of several thousand *G. sepium* planted there for vanilla production (Allen & Allen 1981, The Leguminosae: A source book of characteristics, uses and nodulation, Univ. of Wisconsin Press, Madison, Wisconsin, 812 pp.). The caterpillars were placed in a clear-plastic bag, along with cuttings of *G. sepium*, for rearing to adulthood.

A thorough search of the *G. sepium* having the caterpillars revealed no other individuals of *P. hipparchia,* as was also the case for an additional eight trees of this species examined in the same area. Both caterpillars were discovered on the dorsal (upper) exposed surfaces of old, tough leaves (Fig. 1), and about 1 m apart at eye level (about 1.8 m above the ground). At the time of discovery, the majority of *G. sepium* trees at the site were without flushes of new (fresh) leaves. From a distance of about 1 m, the caterpillars resembled curled, dry leaves (Fig. 1).

Within three days after collection, both caterpillars molted to the final instar, exhibiting little change in overall appearance from the previous instar. The final instar lasted only a few days; both caterpillars formed loose silken cocoons in the leaves by 7 March. Each cocoon (Fig. 1) consisted of a thin sheet of silken mat across several leaves, and dorsally mostly the larval tubercles shed during spinning. The pupal stage lasted about one month (under laboratory conditions of 65–70°C and 30–40% RH). Both adults emerged between 1500–1600 h. One was female, the other a male (Fig. 1).

At the time of discovery, the caterpillars were both about 24 mm long and 20 mm wide, including the greatest expanse of the laterally positioned "horns" (Fig. 1). When the caterpillar was motionless on a leaf, the horns were held laterally against the leaf surface (Fig. 1). When moving, the caterpillar appeared to be rocking back and forth, with a slight rotation of the horns. The squarish, angular body profile of a motionless caterpillar on a leaf (Fig. 1) became spherelike when the caterpillar was disturbed: the caterpillar curled itself into a ball, and partially tucked in and interlocked some of the lateral horns. Several sustained prods with a forceps were needed to ellicit this curling behavior.

The overall color of the caterpillar consisted of a patchwork of brown shades. Cramer (1791, Uitlandsche Rupsen, Supplement) reported the larva (Plate XVIII) of *P. hipparchia* to be light-brown in color. As in all Limacodidae, the head capsule (about 4 mm diam) was small and hidden at all times. Both the head capsule and thoracic legs were glossy orange. The first two thoracic segments were almost translucent, and without prominent tufts of setae or lateral extensions of the cuticle. The third thoracic segment had a ringlet of six bulbous, orange tufts of hairs. The lateral horns were present on the first three abdominal segments (one pair per segment), and dorsally were darker brown than below. The horns of the third segment were dorsally more markedly brown than those of the previous two segments. Those of the fifth abdominal segment were dark brown dorsally, while those of segments 7–9 were light brown (tan) dorsally. No lateral horns were present on abdominal segments 4 and 6. The lateral horns appeared to be extensions of the cuticle, and were covered with short setae (see Dyar 1896, J. New York Entomol. Soc. 4:167–190). Dorsally, each abdominal segment had a dark brown rectan-

FIG. 1. *Phobetron hipparchia*. Left top and bottom: Final-instar caterpillars on leaves of *Gliricidia sepium*. Right top: Cocoon. Right bottom: Reared male (above) and female (below).

gular patch, with a light spot in the center and even darker borders (Fig. 1). A dorsal-medial raised line of tan-colored setae ran lengthwise on both thoracic and abdominal regions. The body of the caterpillar was 8 m wide at the thickest point within a day of cocoon formation. Following cocoon formation there was no noticeable change in the colors of the larval cuticle, even though it became part of the cocoon.

Phobetron hipparchia, the single species of the genus represented in the neotropical region, apparently gets the name "monkey slug" from the curiously shaped caterpillar stage. One of the two North American species of the genus, *P. pithecium* (J. E. Sm.) is the "hag moth," and its caterpillars feed on a broad range of trees, none of which apparently is within the Leguminosae (Papilionoideae) (Covell 1984, A field guide to the moths of eastern North America, Houghton Mifflin Co., Boston, 496 pp.). Dyar (1896, op. cit.) noted that *P. pithecium* larvae perch on the undersides of leaves until the last instar, and that *Phobetron* larvae in general cryptically resemble dead leaves. Even though perched on the upper sides of leaves, the final-instar larva of *P. hipparchia* appears cryptic, resembling the yellow, brown, and green blotch pattern of older *G. sepium* leaves. The observed pattern of cocoon construction, in which cast-off tubercles are added to the silk during spinning, is considered typical by Dyar for New World *Phobetron,* enhancing crypsis of the pupal stage.

Of the several genera and species of North American Limacodidae discussed in Covell, none apparently utilize legumes as larval food plants. Yet an outstanding feature of these moths in general appears to be their highly polyphagous food habits as caterpillars (Dyar 1924, op. cit.; Covell, op. cit.). Several genera and species of Limacodidae feed on legumes in Australia.

McFarland (1979, J. Lepid. Soc. 33: Supplement, 72 pp.) reports that Australian limacoids are associated with *Acacia* and other legume genera, and that caterpillars of some species invariably occur on old, tough leaves and stems of food plants as in the present observations. Within the neotropical region, the limacodid *Sibine apicalis* (Dyar), or "gusano montura," sometimes defoliates banana (*Musa* spp.) trees (Jaramillo & Jimenez 1974, Turrialba 24:106–107). Thus both dicotyledenous and monocotyledenous larval food plants for the Limacodidae are known from the neotropical region. Cramer reported *P. hipparchia* on *Granadilla* (Passifloraceae). *Eucalyptus* spp. (Myrtaceae) are major larval food plants for the Limacodidae in Australia and Africa (McFarland; Sevastopulo 1983, J. Lepid. Soc. 37:91, respectively). But in East Africa some limacodids feed on indigenous legumes (*Acacia* spp.), but not introduced species of the family. *Gliricidia* is endemic to the neotropical region, and given the great evolutionary diversification of the papilionoid legumes in tropical America (Richards 1964, The Tropical Rain Forest, The Univ. Press, Cambridge, England, 437 pp.), one might expect to discover several other legume larval food plants for *P. hipparchia. Gliricidia* is widely distributed throughout the American tropics, both in natural habitats, as a result of its extensive use as a shade tree for cacao and coffee, and as a support for vanilla vines.

In spite of several years of casual observation during both dry and rainy seasons, I did not notice other *P. hipparchia* caterpillars on the trees.

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BOOK REVIEWS

MILKWEED BUTTERFLIES, by P. R. Ackery and R. I. Vane-Wright. 1984. British Museum (Natural History), Cromwell Road, London SW7 5BD, England. v–ix + 425 pp., including 261 figures, 12 colored and 73 halftone plates, quarto size. Price £ 50. Also published in U.S. with Cornell Univ. Press, Ithaca, New York.

The full title of this book, "Milkweed butterflies: their cladistics and biology, being an account of the natural history of the Danainae, a subfamily of the Lepidoptera, Nymphalidae" states the goals of Ackery and Vane-Wright's study. They succeed admirably in this difficult task. While the major thrust of the book is a taxonomic revision of the danaines, there is a wealth of well documented biological information about distribution, behavior, life history, chemical attraction and defense, genetics, ecology, mimicry and faunistics. This makes the book not only valuable to the systematist, but also to the worker in other biological disciplines.

The fact that the revisionary section is a cladistic study probably will bother pheneticists and at least some evolutionary taxonomists, but this does not concern the authors. It is reassuring to see a study that is done strictly on characters, and draws no systematic conclusions not supported by those data; the authors freely admit that certain relations are not shown by the characteristics they used, and suggest that these problems may be solved later by the addition of new characters. What is speculation by the authors is clearly so labeled, and definitive statements are not made without reference to underlying reasons. The revision is, therefore, highly scientific; and it is a pleasure to have the authors lead one through the reasoning to their conclusions without the appearance of the occult that one is so often left with in systematic revisions where conclusions are "correct" simply because authors state they are.

The cladistic section of the book involves discussions of the characters treated and the classification scheme derived from them. Each character is discussed, numbered in the text and, perhaps most importantly, is illustrated clearly in the figures, along with alternate character states. Again, one can follow the reasoning through a logical progression to the classification adopted. There are some valuable, but unconventional, thoughts on classification intertwined with the data, such as those on clades and polytypic species (pp. 20–22), including the concepts of "cladospecies" and "paraspecies", and those immediately following on larval versus adult characters. Their suggestions for further systematic research on the danaines (pp. 61–66), most of which the authors promise to tackle later are valuable and thought-provoking. The book would have been even more useful had it considered the myriad subspecies, but an attempt to analyze cladistically some 2,000 names would have been humanly impossible, and the result would not have been economically feasible to print. Nevertheless, the handling of the subject is reasonable enough to make a confirmed cladist of the reader: if only people of that taxonomic school were always so rigorously tied to logic!

The authors anticipated that the revision might be controversial because it upsets prevailing nomenclature. Ackery and Vane-Wright comment about the genus *"Danaus"* of authors. *"Danaus"* is at best a grade taxon and is probably polyphyletic, perhaps paraphyletic. A number of species are placed in genera far removed from their "conventional" placement, but the authors recognize the difficulty that others might have accepting these new assignments, stating (p. 8), ". . . because of the still overriding influence of 'Seitz' and the acceptance of *'Danaus'*, we can be sure that a dual nomenclature, with *'Danaus' sita* for *Parantica sita*, *'Danaus' similis* for *Ideopsis similis*, *'Danaus' hamata* for *Tirumala hamata* and so on, will unfortunately continue in existence for a considerable length of time—probably until about A.D. 2179 judging by past performances!" Such a statement might be made about any revision that accepts a different nomenclature than that in a "standard" work, but Ackery and Vane-Wright present a large and impressive body of data, and it is up to their detractors (if any) to examine such data in detail and show where they think the authors are wrong. I hope Ackery and Vane-Wright are incorrect on the period of time until their nomenclature is accepted.

Ackery and Vane-Wright have gathered an impressive array of biological data on the danaines which are summarized in Part 2: Biology (pp. 67–102). They have also generated a large body of data on co-mimicry and faunistics (pp. 103–158). Both of these sections should be of great interest to ecologists, evolutionists and other nontaxonomists, as well as to systematists in the broadest sense. Part 4 consists of identification keys, often utilizing novel characteristics not stressed in the typical key; and all data are summarized in Part 5, the specific taxonomic and biological catalogue (pp. 173–245), an impressive compendium of information that should convince even the most skeptical. There are some new synonyms, combinations and taxa, but finding them requires some searching because they are buried throughout the text. Short of a section summarizing changes, there is no other way the data could have been presented conveniently. A short addendum follows, and precedes an exhaustive bibliography of 36 pages.

The work is remarkably free of typographical errors—the one I noticed was the rendering of Japan as "Japen" on p. 21. It is an attractive book and easy to follow. The illustrations are uniformly of high quality, including line drawings, colored plates, halftone plates, and 394 additional figures illustrating all aspects of danaines and their biology. Colored plates depict some danaine mimetic associations in the Philippine and Indonesian Islands. It is too bad that illustrations are not cross-referenced to the pages on which descriptions occur (the pages with descriptions do have references to plates), but this is a minor complaint; also each species is mentioned several times in the text, and to which page would the plate reference refer? The comprehensive Index clearly leads the reader to any place a taxon is discussed.

I must consider this work to be one of the major taxonomic revisions of this century, and it is a good book for the reader who is not taxonomically inclined. The authors have attacked a problem, solved much of it, and have honestly admitted those parts that have resisted solution so far. To say that I am impressed with this work is an understatement; it is the kind of work that one always hopes to be able to do. The book, even though expensive, is well worth the cost; I would recommend it to anyone interested in well explained and defended cladistic analyses, in systematics of Lepidoptera, or in the Danainae.

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A MONOGRAPH OF THE BIRDWING BUTTERFLIES. Volume I, parts 1–3, the subgenera *Aetheoptera, Ornithoptera, Schoenbergia*; Volume II, parts 1–2, the genera *Trogonoptera, Ripponia, Troides* (partim), by J. Haugum and A. M. Low. Vol. I. 308 pp., 12 plates. Vol. II. 240 pp., 12 plates. Scandinavian Science Press, Ltd., Klampenborg, Denmark. 1978–1984.

No other group of butterflies has attracted as much attention or interest as the birdwing butterflies. In this two-volume set, the authors provide the most detailed analysis of these showy butterflies to date. The first part of Vol. I, for example, on *Aetheoptera,* deals with only two species, yet numbers 84 pages; and Vol. II, part 1, which describes three species, numbers 104 pages. The text of this work will complement the beautiful illustrations in the recently published Birdwing Butterflies of the World, by B. D'Abrera.

Volume I covers the genus *Ornithoptera,* Volume II, *Trogonoptera, Ripponia,* and *Troides.* The genera and species are introduced with descriptions and notes on biology, followed by keys. However, no keys are given for most subspecies, which means that most (as with so many subspecies of butterflies) must be determined by geographic locality. Each species and subspecies is described in detail, and notes are given on the phylogenies of each taxon. Several illustrations, including distribution, accompany the description of each taxon. The authors tend to recognize almost every described taxon, and include descriptions of several "forms" or aberrations. Even though the authors recognize that formal names given to such infraspecific forms are not nomenclaturally valid, I find it annoying to see several new names applied to these forms.

A group as well known and as popular as the birdwing butterflies is bound to generate controversy in the literature, and such is the case here. I found the authors to be particularly critical of D'Abrera, often disagreeing with what is said in his volume. For example, D'Abrera recognizes only two subspecies of *Ornithoptera goliath,* Haugum and Low, five. D'Abrera considers *O. richmondia* and *O. urvillianus* separate species from *O. priamus,* not so Haugum and Low. *Ripponia* is used for *hypolitus,* but D'Abrera considers it a *Troides.*

For all the detailed analysis given for each subspecies, I find it disappointing that no quantitative data were used to back up the authors' assertions that these taxa are, indeed, taxonomically distinct. Most of the diagnostic comments are qualitative, as two examples will show: Males of *O. tithonus* "*waigeuensis* may be recognized by having a narrow HW [hind wing] with a notable reduction of the apical area; the wing is even further modified and less angular at the apex than in subspecies *misresiana* and *tithonus* . . . ," and "The male HW [of *T. amphrysus ruficollis* f. loc. *euthydemus*] tends to be more rounded than in *ruficollis* on average, also the FW [fore wing] may be broader . . . ," which means to the reader that geographic locality will still be the only way to identify subspecies.

Puzzling also is the uneven treatment of "Material examined." For some species, a detailed listing is given, for others, the data are incomplete, as for *O. goliath atlas*: "photographs of a further series of E. Weyland Mts. imagines" [how many?]. The locations of types are, unfortunately, not addressed for all taxa. No cladistic analysis was carried out on this group, although I hope the authors may consider this in their final volume.

The books are handsomely bound, the printing, layout, and illustrations are good, but, alas, errors in typography and syntax abound. The color photos of Vol. I are excellent, but those of Vol. II have a white halo within the marginal black areas of the wings figured.

Despite their shortcomings, these volumes represent the best compilation of data for these magnificent butterflies. As one who is fascinated by these gorgeous insects, I heartily recommend this work for every lepidopterist interested in Old World Papilionidae.

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OBITUARIES

Arthur C. Allyn (1913–1985)

Dr. Arthur Cecil Allyn, life member of the Lepidopterists' Society and Director Emeritus of the Allyn Museum of Entomology, died on 22 March 1985, after a lingering illness. He will be remembered by the lepidopterological community for his generosity, dedication, and service to the science.

Dr. Allyn was born in Evanston, Illinois on 24 December 1913, completed primary and secondary schooling there, and attended Dartmouth and Beloit Colleges. He received a D.Sc. from the University of Florida in 1981 in recognition of his accomplishments in and service to entomology. He is survived by his wife, Dorothy D. Allyn, and three children, David D. Allyn, William N. Allyn and Dorothy A. Lavick, as well as eight grandchildren.

Dr. Allyn had a successful and diversified business career with international interests in oil, maufacturing, farming and sports in many countries, including Australia, Indonesia, Canada, South Africa and countries in Latin America. He was a philanthropist of note, being responsible for a wing at Chicago's Mercy Hospital and the Convention Center and Robarts Sports Arena in Sarasota. He was interested in the arts, especially theater, and he and his wife coproduced a number of plays at the Asolo State Theater in Sarasota. But, his abiding interest was in lepidopterology, and he amassed a huge collection of these insects. Finally he decided that the chore was too much for one man part-time; thus began our association with him in 1968.

Arthur Allyn's interest in Lepidoptera and his desire to establish a quality institution for their study led to the formation of the present-day Allyn Museum of Entomology. During the early days of the Museum, Dr. Allyn continually purchased material that was needed to enhance the Museum collections, often obtaining entire collections or entire season's catches from people throughout the world. Later, collections or individual

specimens were donated to the museum, and less material was purchased, but the growth of the collection continued to its present size of about 850,000 specimens from throughout the world. Dr. Allyn insisted that the collection be worldwide and accepted the necessity of long series of specimens to show individual variation within taxa.

In 1973 the Museum moved to its present home, and it became apparent that it would outgrow the new collection range rapidly if something were not done. Dr. Allyn had been impressed by the compactor housing the collections at the Missouri Botanical Gardens, and we immediately decided that the museum needed such housing. Thus was installed the first entomological compactor in the United States, a system that served as the model for similar systems elsewhere in this hemisphere. It was an excellent choice.

Concern about the backlog of papers in many lepidopterological journals led to the founding of the *Bulletin of the Allyn Museum* late in 1971. This publication, patterned after *American Museum Novitates*, has gone through 105 numbers as of this writing, with indices after every 20 numbers. The *Bulletin* rapidly evolved into a refereed publication, but final responsibility for the content of numbers rests with individual authors.

Dr. Allyn became an accomplished scanning electron microscopist largely through his own efforts. One of his photographs was featured on the cover of an issue of *Annals of the Entomological Society of America*. After studying a number of entomological papers with which he disagreed, based on his knowledge of the physical sciences, he began to publish papers on structures of Lepidoptera not only with Museum staff, but also with such authors as Dr. John C. Downey, Dr. Miriam Rothschild and Professor David Spencer Smith. Other papers were in varying degrees of completion at his death, some of which may appear in future *Bulletin* numbers. Those papers that were published are standards for the field, and it is a tribute to Arthur Allyn and his coauthors that they are frequently cited not only in lepidopterological, but also in sources oriented toward scanning electron microscopy. Dr. Allyn also cooperated with various researchers in other fields, and his photographs have appeared in publications on optic, muscular and nervous systems of both vertebrates and invertebrates. A complete listing of Dr. Allyn's publications is given in the *Bulletin of the Allyn Museum*, number 97.

Eventually, Dr. Allyn began to search for an orderly transition from the independent nature of the Allyn Museum of Entomology to a more structured, but secure status to assure its permanence. After examining many options, he presented the Board of Directors of the Allyn Museum with a proposal from the University of Florida Foundation which was accepted, and the Museum became a part of the Florida State Museum in 1981. Eventually the present facility will be moved to Gainesville, and the Museum's metamorphosis will be complete.

Arthur Allyn was a benefactor of the Lepidopterists' Society in numerous ways. In the late 1960's, the Society faced severe financial difficulties from which Dr. Allyn rescued it in return for financial accountability from the officers. Through a series of excellent treasurers, the Society has managed to remain a viable entity ever since. Equally important was the establishment of the Karl Jordan Medal for papers of lepidopterological excellence. There have been ten Jordan Medal awards since 1973, and the award winners have been truly international. Not only is the United States represented by Jordan Medal laureates, but also France, Canada and England.

Those of us who were close to Arthur Allyn will miss him for his generosity, excellent judgment and common sense. He would not want this, however, to become an overriding emotion: he would demand that we continue as before. Lepidopterology, along with many other pursuits, is better for its association with him.

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Lionel George Higgins (1891–1985)

With the recent death of Lionel Higgins, at the age of 94, one of our few remaining links with pre-War entomology has been severed. Perhaps reflecting those more leisurely times, in common with many of his generation he was a "generalist" of distinction, equally at home in art and music as in his chosen profession of medicine, or indeed entomology. Following rheumatic fever in childhood, Lionel was pronounced too delicate for a formal school education. As a result, the interests that so enlivened his lifetime were probably kindled. Taking a medical degree at Clare College, Cambridge, he qualified at St. Thomas' Hospital before serving in the 1914–18 War as a surgeon-lieutenant. Specializing in gynaecology and obstetrics, he practiced from 1922 onwards in Woking, Surrey, where he continued to live after his retirement.

In the field of Lepidoptera, he is, of course, best known for his collaborative book with the late N. D. Riley, "A Field Guide to the Butterflies of Britain and Europe" (1970), a standard work translated into at least nine languages, with world-wide sales approaching 200,000; and its companion volume "The Classification of European Butterflies" (1975). These works were the culmination of fifty years of serious study. While this is not the place to include a full bibliography, C. R. Smith (Type specimens of the taxa described by L. G. Higgins in the British Museum (Natural History), in preparation) lists more than 70 titles, which truly reflects his contribution since 1924, when the first work appeared. Probably he would have regarded the Melitaeinae as "his" group. Major contributions in 1941, 1950, 1955, 1960, 1978 and 1981 provided a firm foundation for future work. Tangible recognition of his contributions to natural history include the Stamford Raffles Award (Zoological Society of London) and the H. H. Bloomer Award (Linnean Society).

As well as being a prolific author, he was an indefatigable collector, both of butterflies and books. Accompanied by his wife, Nesta, he collected extensively in the holarctic

region. As recently as 1978, shortly before his wife's sad and unexpected death, they were to be found wielding their nets in the mountains of Kashmir! The British Museum (Natural History) is the direct beneficiary—his incomparable collection in excess of 30,000 specimens was generously bequeathed to this Institution. As for his library, much passed to the Hope Entomological Collection, Oxford; but over the years, many volumes were presented to the BM(NH), including several rare works by Jacob Hübner.

Despite Lionel Higgins' eminence, it must be acknowledged that some of his ideas attracted criticism. Aware of this, he maintained a dignified, but never dogmatic, confidence in his convictions. In methodology, he was a man of his times (few of us could claim to be anything else!). While the numerical and cladistic revolutions passed him by, he remained true to his basic principles—overall similarity and the equivalence of species-groups and genera. It is impossible to predict how the future will judge his work, but personal experience suggests that the results of "traditional" methods should be treated with the utmost respect.

How can the loss of such a man be measured? A glance at his correspondence file gives some indication. There can hardly be a lepidopterist of note who has not communicated with him over some problem. All were given the benefit of his lifetime's experience. The personal touches perhaps give most indication of the esteem and affection in which he was held: photographs sent by correspondents, showing themselves and sometimes their families, at ease in their homes. For me, the abiding memory will be of a battered briefcase, a cork postal-box containing the latest treasure from the Pamirs or Urals, and above all the half serious admonition, always delivered with a twinkle in the eye, that I really should learn something about palaearctic butterflies.

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of the

LEPIDOPTERISTS' SOCIETY

THE LEPIDOPTERISTS' SOCIETY

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The object of the Lepidopterists' Society, which was formed in May, 1947 and formally constituted in December, 1950, is "to promote the science of lepidopterology in all its branches, ... to issue a periodical and other publications on Lepidoptera, to facilitate the exchange of specimens and ideas by both the professional worker and the amateur in the field; to secure cooperation in all measures" directed towards these aims.

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Cover illustration: First stage larva of *Natada nasoni* (Grote) (Limacodidae), from Dyar 1899, J. New York Entomol. Soc. 7: 61–67. Suggested by Marc E. Epstein.

WHY *PIERIS RAPAE* IS A BETTER NAME THAN *ARTOGEIA RAPAE* (PIERIDAE)

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ABSTRACT.   We show that there is no phylogenetic justification for changing the name of *Pieris rapae* to *Artogeia rapae*. We "define" *Pieris* by the presence of androconial basal lobes, and suggest that this grouping, which includes *P. rapae*, *P. brassicae*, and *P. napi*, is monophyletic. Female genital characters indicate that *Perrhybris, Itaballia,* and *Ganyra* are the closest relatives of *Pieris*. We discuss criteria for choosing generic nomenclature, and suggest that the following guidelines will best promote nomenclatural stability. If a genus is monophyletic, do not change the name. If a genus is not monophyletic, choose the combination of monophyletic generic groupings that will create the fewest name changes. If another option causes more name changes now but will be more stable in the future because of better evidence for monophyly, then present the reasons and evidence for that choice.

Pieris rapae Linnaeus is one of the best known and commonly encountered temperate area butterflies. Although native to the Palaearctic, it is now nearly ubiquitous in suitable disturbed habitats in North America (Howe 1975), New Zealand (Gibbs 1980), and Australia (Common & Waterhouse 1981). Because *P. rapae* is widely distributed, easily reared, and a pest on cultivated crucifers, it has been extensively studied in the agricultural, ecological, and physiological literature (Harcourt 1966, Dempster 1969, Aplin et al. 1975, Slansky & Feeny 1977, Blau et al. 1978, Kobayashi & Takano 1978, Yamamoto & Ohtani 1979, Wolfson 1980, Chew 1981, Jones et al. 1982, Gilbert 1984, Maguire 1984).

The generic placement of *P. rapae* has recently been changed from *Pieris* to *Artogeia* Verity. Schrank (1801) placed *rapae* in *Pieris* when he originally described the genus, and Klots (1933) retained this generic

placement in his systematic treatment of world Pieridae. Verity (1947) proposed *Artogeia* as a subgenus including *rapae*, and Kudrna (1974) and Higgins (1975) elevated it to generic rank, an action that has been followed in some general works (Pyle 1981, Miller & Brown 1981) but not others (Kawazoé & Wakabayashi 1976, Opler & Krizek 1984). This situation was further complicated when Kudrna later treated *Artogeia* as a subgenus (Blab & Kudrna 1982), and Feltwell and Vane-Wright (1982) suggested that *Artogeia* might not be monophyletic.

In this paper we assess the evidence for switching *rapae* from *Pieris* to *Artogeia*. We took up this project because of repeated inquiries from scientists in a variety of biological disciplines to the National Museum of Natural History concerning the proper generic name for *rapae*. We address the following questions: "What is the evidence for the change in generic nomenclature and is it compelling?", "What is the 'best definition' for *Pieris*?", "What are the closest relatives of *Pieris*?", and "What criteria will promote stability of generic nomenclature?"

It is not our intent to produce a definitive work on *Pieris* systematics. Besides reporting the results of a few representative female genitalic dissections, we discuss published information only, all of which was available to Kudrna and Higgins, with the exception of two recent papers on isozymes. We discuss characters sequentially, note their states and distributions, and generally limit our discussion to those species for which we have information. Many species level decisions, particularly in the *P. napi* group, are controversial (Warren 1961, Bowden 1972, Eitschberger 1983, Geiger & Scholl 1985); we avoid entering the fray because it is largely irrelevant to our purpose. Finally, we show that treatment of all *Pieris* species would not alter our conclusions.

Pieris rapae or *Artogeia rapae*

In this section, we ask whether *rapae* is more closely related to *napi* Linnaeus—the type of *Artogeia*—or to *brassicae* Linnaeus—the type of *Pieris*. The classification of Kudrna (1974) and Higgins (1975) implies that the former is correct, while others (Mariani 1937, Geiger 1981, Geiger & Scholl 1985) suggest the opposite. These two possibilities are represented by alternative phylogenies (Figs. 1 & 2).

To determine primitive character states among these species (the state at point A in the phylogenies), we used two sets of outgroup species. The first set is *Pontia daplidice* Linnaeus and *Synchloe callidice* Hübner. Pierid specialists (Klots 1933, Bernardi 1947) considered them to be closely related to the *brassicae-napi* complex, and sometimes included them in *Pieris*. Kudrna (1974) placed them next to *Pieris* and *Artogeia*. They are the immediate outgroups of the *brassicae-napi* lineage in dendrograms constructed from isozyme data (Gei-
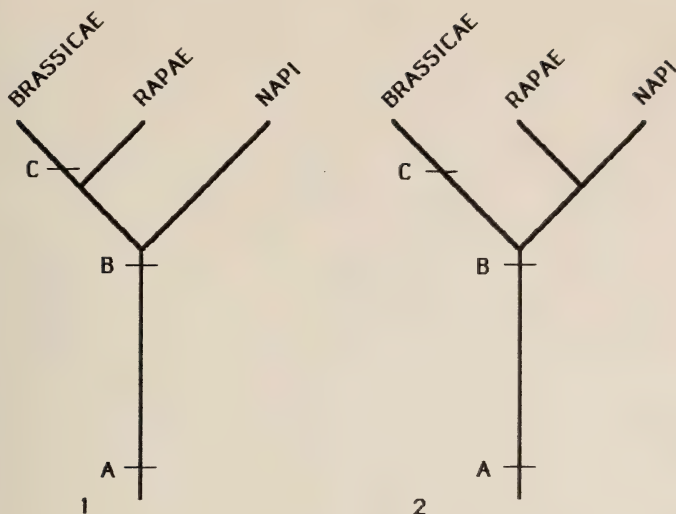
FIGS. 1 & 2.   Phylogenies showing cladogenesis among *Pieris brassicae*, *P. rapae*, and *P. napi*. The letters designate ancestral species in the branching sequence.

ger 1981, Geiger & Scholl 1985). The second outgroup set is *Ganyra* Billberg, *Itaballia* Kaye, and *Perrhybris* Hübner (*sensu* Klots 1933). We discovered that they share female genitalic characters with the *brassicae-napi* complex (detailed below), and may be more closely related to them than has been previously realized.

The first character that Kudrna (1974) and Higgins (1975) used in their taxonomic analysis was androconial structure (illustrations in Dixey 1910, 1932, Bernardi 1947, Warren 1961). There are four major shapes in the "*Pieris* group" with slight quantitative interspecific variation within each type: *P. brassicae* has one type of androconium (Fig. 3), *rapae* and *A. napi* a second (Figs. 4 & 5), outgroups *P. daplidice*, *Perrhybris*, and *Itaballia* a third (Figs. 6 & 7), outgroup *Ganyra* a fourth (Fig. 8), and outgroup *S. callidice* lacks androconia. On either phylogeny this distribution of character states can be explained, no matter which outgroup state occurred at point A, by the *rapae-napi* androconium evolving at point B and the *brassicae* androconium evolving at point C. Although there are other equally parsimonious possibilities, either phylogeny could produce the distribution of character states simply—each androconium type evolved once. Thus, although *rapae* and *A. napi* share a similar androconial structure, this distribution provides no evidence for choosing between the phylogenies in Figs. 1 and 2.

Kudrna (1974) and Higgins (1975) also used male genitalic charac-
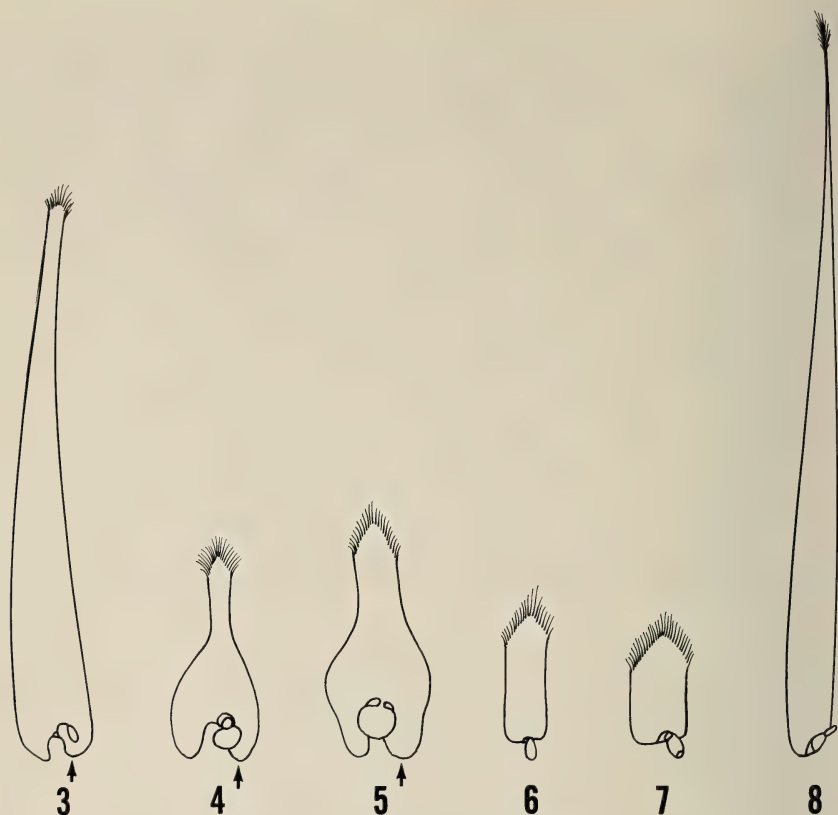
FIGS. 3–8.   Outlines of androconia, redrawn from Dixey (1932). Arrows in first three figures point to the right basal lobe. **3,** *Pieris brassicae*; **4,** *P. rapae*; **5,** *P. napi*; **6,** *Pontia daplidice*; **7,** *Itaballia demophile*; **8,** *Ganyra josepha*.

ters for defining *Artogeia*. The male genitalia of *A. napi* and *rapae* are similar to each other, and differ from *P. brassicae* (illustrated in Klots 1933, Bernardi 1947, Kudrna 1974, Higgins 1975). The penis of *P. brassicae* has a dorsal hump and each valva has a distal pointed process while *rapae* and *A. napi* lack the dorsal hump and the process. The outgroups, like *rapae* and *A. napi,* lack a penial dorsal hump and process on the valva (except for *Ganyra,* which has a differently shaped valva process). Thus, the *P. brassicae* penis and valva morphology is derived, defines only *P. brassicae* (evolved at point C on either phylogeny), and provides no information about the phylogenetic position of *rapae*.

Higgins (1975) also used haploid chromosome numbers to differentiate *Pieris* from *Artogeia*. Reported haploid chromosome numbers (De
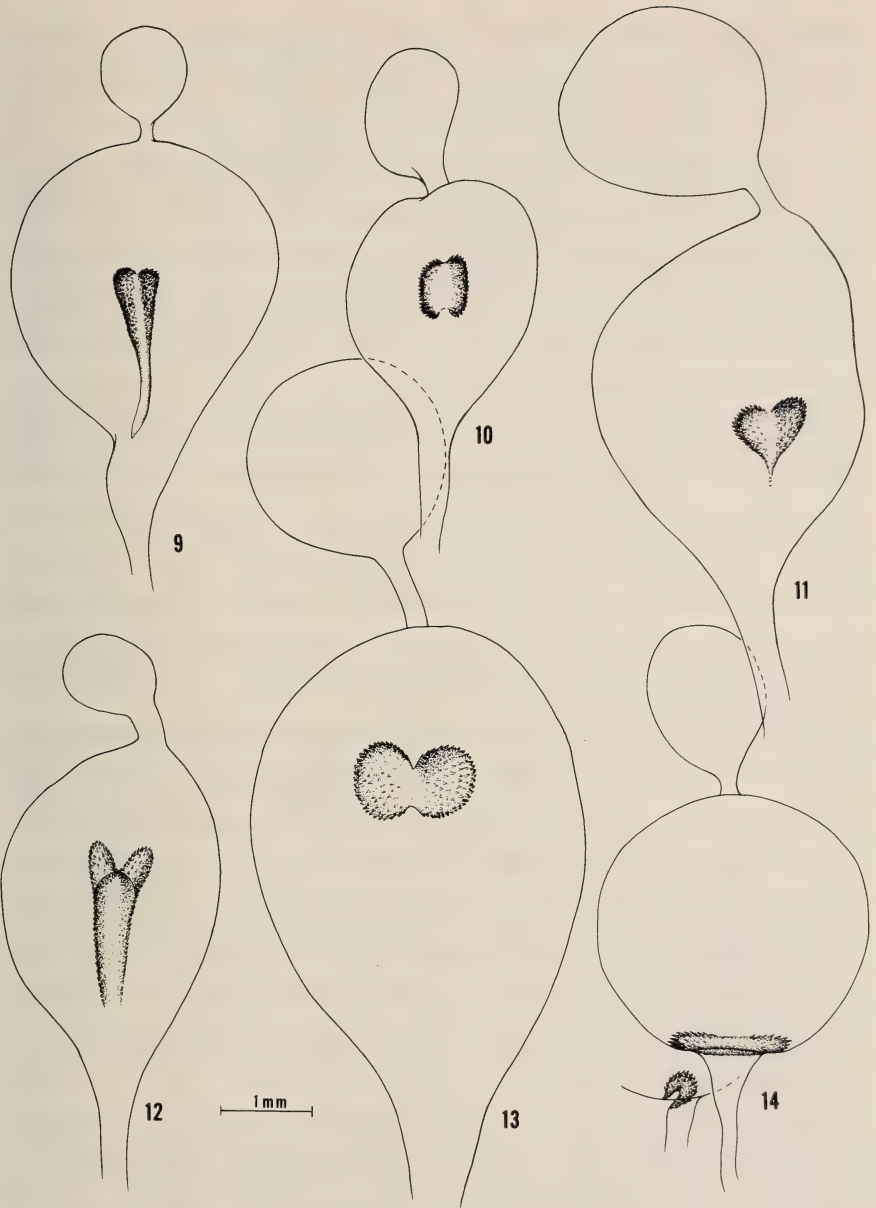
FIGS. 9–14. Right dorsolateral view of the corpus bursae and anterior portion of the ductus bursae (except for *Pontia callidice,* which is a dorsal view with an additional lateral aspect of the cervix). **9,** *Pieris napi;* **10,** *P. rapae;* **11,** *P. brassicae;* **12,** *Perrhybris pyrrha;* **13,** *Ganyra josepha;* **14,** *Pontia callidice.*

Lesse 1967, 1970, De Lesse & Brown 1971, Robinson 1971) are *P. brassicae*—15, *rapae*—25–26, *A. napi*—25–28, and for the outgroups *P. daplidice*—26, *S. callidice*—26, *Itaballia*—25–26, and *Perrhybris*—27–29. We infer that the lower haploid chromosome number of *P. brassicae* is a derived character state that defines only *P. brassicae*—it evolved at point C in the phylogenies—and that provides no information on the systematic position of *rapae*.

Since the characters used by Kudrna (1974) and Higgins (1975) provide no evidence for choosing between the phylogenies in Figs. 1 and 2, the placement of *rapae* in *Artogeia* was phylogenetically unjustified. We now ask whether other published characters provide information on the generic placement of *rapae*.

Mariani (1937) and Bernardi (1947) examined "*Pieris*" female genitalia, and reported interspecific variation in morphology of the single signum (often called "lamina dentata" in the pierid literature) on the corpus bursae. The signum of *A. napi* has a long posterior process ("flagello" of Mariani, "tail" of Chang [1963]) that is lacking in *rapae* and *P. brassicae* and in all outgroup species (Figs. 9–14, figures in Mariani and Bernardi). Thus, the posterior process is a derived character state that apparently evolved once on the lineage leading to *A. napi*, and does not give us information with which to distinguish the phylogenies in Figs. 1 and 2.

Geiger (1981) and Geiger and Scholl (1985) electrophoresed enzymes from species of *Pieris*, *Artogeia*, *Pontia*, and *Synchloe*, but not for the other outgroups. They obtained a dendrogram of relationships by using an unweighted pair-group average clustering method on genetic similarities. They found that *rapae* is more similar to *P. brassicae* than to *A. napi* and that all three are more similar to each other than to *Pontia* and *Synchloe*. This result supports the phylogeny depicted in Fig. 1. There are numerous methods for coding and analyzing electrophoretic data, and Mickevich and Mitter (1981) propose criteria for judging different methods. Before uncritically accepting their dendrograms, we would want to know if other methods of coding and analysis corroborate their results.

In summary, analysis of published characters indicates that the use of *Artogeia* as a genus or subgenus including *rapae* is phylogenetically unjustified. Although the male genitalia, androconia, and haploid chromosome numbers of *rapae* are more similar to *A. napi* than to *P. brassicae*, the opposite relationship is true with regard to the female genitalia and isozymes. Further, these similarities are based on primitive character states, as Feltwell and Vane-Wright (1982) had predicted, and do not provide the information necessary to choose between the phylogenies in Figs. 1 and 2. Characters of "*Pieris*" immature

stages may provide the information necessary to decide this point, but have not been used in *Pieris* revisions.

THE GENUS *PIERIS*

Since *rapae* is such a widely known species and since Kudrna and Higgins' concept of *Pieris* and *Artogeia* leave *rapae* without certain generic placement, we ask in this section whether there are other, more reasonable definitions for *Pieris*. Klots (1933) revised the world pierid fauna. Although he narrowed the definition of *Pieris*—it previously had been a catchall genus for many questionably related pierines—subsequent authors have split the genus further. We ask whether any of these groupings are monophyletic. For outgroup comparisons, we use those genera that Klots considered to be most closely related to *Pieris*: *Leptophobia* Butler, *Itaballia*, *Perrhybris*, *Ascia* Scopoli (including subgenus *Ganyra*), *Tatochila* Butler, *Phulia* Herrich-Schäffer, and *Baltia* Moore.

Three different concepts of *Pieris* besides that of Kudrna and Higgins have been used since 1933. For ease of communication, we list representative species for each grouping, and refer the reader to the original work for a complete list. Klots (1933) placed *brassicae, rapae, napi, callidice, daplidice,* and *pylotis* in *Pieris*. Mariani (1937) and Bernardi (1947) put the first four of these species in *Pieris*, while Higgins and Riley (1970) restricted *Pieris* to the first three. (Note that Higgins [1975] later narrowed the genus further, like Kudrna, to include only *brassicae* and close relatives.)

Klots (1933) defined *Pieris* with a paragraph of character states. For the most part, however, they are too ambiguous to code accurately. For example, how does one code "antenna long, with abrupt club" (*Pieris*), "antenna long, with usually somewhat abrupt club" (*Ascia*), and "antenna long, with flattened abrupt club" (*Tatochila*)? Further, each of Klots' generic character states is shared with at least one outgroup genus. Because of character state ambiguity and the lack of unique, potentially defining character states, we found no evidence in Klots' work to indicate that his concept of *Pieris* is monophyletic.

Mariani (1937) and Bernardi (1947) apparently ignored *pylotis* (a neotropical species that does not "look" like other *Pieris* species) and moved *daplidice* to *Pontia*. *Pontia daplidice* has forewing veins R_3 and R_{4+5} fused while they are separate in the other *Pieris* species. Outgroups *Phulia* and *Perrhybris* have the fused veins while the other outgroups have separate veins (Klots 1933). Because both character states are found in the outgroups, the primitive character state is ambiguous. Phylogenetic interpretation of this character is thus equivocal.

Higgins and Riley (1970) joined *callidice* with *daplidice* in *Pontia*,

so that their *Pieris* grouping consisted of *brassicae, rapae, napi,* and close relatives. The androconial lateral edges of these species and their close relatives protrude basally to form lobes (Dixey 1932, Bernardi 1947, Warren 1961) (Figs. 3–5) while the androconial basal edge is flat in *daplidice* and relatives (Bernardi 1947) (Fig. 6), *pylotis* (Dixey 1932), and all outgroup genera (Dixey 1932) (Figs. 7 & 8). Since *daplidice* and *pylotis* share the primitive state—that which occurs in the outgroup genera—the androconial basal lobes would appear to be a derived, defining character for the *brassicae-napi* complex. This situation contrasts with the one in the previous section, in which *rapae* and *napi* share an androconium type that does not reflect phylogenetic relatedness because *brassicae* does not possess the primitive character state.

We "define" *Pieris* by the androconial basal lobes. Although we are reluctant to define a genus on the basis of one character state, there are no alternatives in this case. From published illustrations of androconia (Dixey 1932, Bernardi, 1947), we place the following specific taxa—listed in Bernardi—in *Pieris*: *brassicae, deota* de Niceville, *brassicoides* Guerin, *krueperi* Staudinger, *tadjika* Groum-Grshimailo, *canidia* Sparrman, *manni* Mayer, *rapae, dubernardi* Oberthur, *extensa* Poujade, *stoetzneri* Draeseke, *napi, virginiensis* Edwards, *ochsenheimeri* Staudinger, *ergane* Geyer, *melete,* and *davidis* Oberthur. Although there are other taxa, particularly in the *napi* group, that are given specific rank by some authors, we leave species level decisions to others.

We believe that this grouping is the most reasonable and stable one for *Pieris*. There is an enormous biological literature on *Pieris brassicae, Pieris rapae,* and *Pieris napi,* and the name *Pieris* is widely recognized by nontaxonomists in connection with these species. Our grouping will preserve this association, and because it is based on the best available evidence for monophyly, it is most likely to be stable in the future.

There are three morphologically distinct groups within *Pieris*. The *P. brassicae* group (*brassicae, deota, brassicoides*) has the androconial and male genital structures of *brassicae,* and is probably a monophyletic lineage defined by these structures. The *P. napi* group (*napi, virginiensis, ochsenheimeri, ergane, melete, davidis,* and presumably *stoetzneri, extensa,* and *dubernardi*—Bernardi [1947]) has a posterior process on the signum, which probably defines this group as a monophyletic lineage. The *P. rapae* group (*krueperi, tadjika, canidia, manni, rapae*) lacks derived character states. There is no evidence to indicate whether it is monophyletic or whether it is phylogenetically more closely related to the *P. brassicae* or *P. napi* groups. Thus, even if we had examined all *Pieris* species in the previous section, it would

not have provided us with evidence on the phylogenetic position of *P. rapae*. Interestingly, the same three groups result when isozyme data are analyzed phenetically (Geiger & Scholl 1985).

THE RELATIVES OF *PIERIS*

In this section we ask which genus or genera are most closely related to *Pieris*. From the work of Mariani (1937) and Bernardi (1947), it appeared that the bursa copulatrix, particularly signum location and shape, had states that might provide information on the phylogenetic position of *Pieris*. Because this character was promising, but unrecorded for many of the outgroups, we dissected the female genitalia of species in *Pieris* and related genera.

We recorded three character states of the bursa copulatrix. In the first, the signum is a narrow transverse band located at the posterior end of the corpus bursae just around the entrance to the ductus bursae (Fig. 14). We recorded this state in *Pontia* (*daplidice, protodice*), *Synchloe* (*callidice*), *Leptophobia* (*eleone* Hewitson, *aripa* Boisduval), and *Ascia* (*monuste* Linnaeus). It also occurs in *Tatochila, Phulia, Baltia,* and close relatives (Field 1958, Herrera & Field 1959, Field & Herrera 1977), in the pierine *Aporia* Hübner (Mariani 1937) and the coliadines *Colias* Fabricius (Mariani 1937) and *Eurema* Hübner (Field 1950).

In the second character state, the signum is located on the right dorsolateral side of the corpus bursae well anterior to the entrance of the ductus bursae (Figs. 9–13). Signum shape varies, particularly in how far it extends posteriorly and in the amount of sclerotization of the median line. We recorded this character state in *Pieris* (*brassicae, rapae, napi, melete*), *Ganyra* (*josepha* Godman & Salvin, *limona* Schaus), *Itaballia* (*demophile* Linnaeus, *viardi* Boisduval, *pisonis* Hewitson), and *Perrhybris* (*pyrrha* Fabricius, *pamela* Cramer [=*lypera* Kollar], *lorena* Hewitson). Mariani (1937) noted its occurrence in all 12 *Pieris* species that he examined.

A third character state is limited to *Glennia pylotis*. There is no signum. The corpus bursae and ductus bursae are greatly modified into a long tube that occupies the length of the abdomen. This tube gradually increases in diameter anteriorly, and the usual abrupt change in size that distinguishes the corpus from the ductus is absent.

The closest relatives of *Pieris* appear to be *Perrhybris, Itaballia,* and *Ganyra*. The position of the signum on the right dorsolateral side of the corpus bursae is an unusual character state that is apparently restricted to these four genera. The other genera that Klots (1933) placed near *Pieris* have the signum at the posterior end of the corpus bursae, which is probably the primitive state for the pierines because it is also

found in the coliadines *Eurema* and *Colias*. A definitive survey of the distributions of female genital structures is obviously desirable.

Those holarctic species that Klots (1933) put in *Pieris*, but which have recently been placed in *Pontia* (Higgins 1975, Miller & Brown 1981) are often considered to be close relatives of *Pieris*. However, we know of no evidence that this group is more closely related to *Pieris* than to other genera, such as *Tatochila*, *Phulia*, and relatives (Shapiro 1979). Further, we have found no published characters to determine whether this group is monophyletic. In short, there is a glaring need for a worldwide treatment of the pierines.

The placement of *Glennia pylotis* remains a problem. Although Klots (1933) treated *Glennia* as a subgenus of *Pieris*, it lacks the androconial basal lobes and signum of *Pieris*. There is currently no evidence to decide whether the divergent female genitalia of *Glennia* evolved from the *Pieris* type or from the *Pontia* type.

STABILITY AND GENERIC NOMENCLATURE

In this section we use the confusion over the generic nomenclature of *P. rapae* as an example to discuss the relationship between taxonomic method and nomenclatural stability.

We suggest that butterfly generic nomenclature can be more objectively chosen than in the past by using the criteria of "stability" and "monophyly". The Preamble to the International Code of Zoological Nomenclature (Int. Comm. on Zool. Nomenclature 1985) states that ". . . the object of the Code is to promote stability and universality in the scientific names of animals . . . ." Ehrlich and Murphy (1982) discuss the widespread support for a stable generic nomenclature.

By monophyly, we refer to taxa defined by derived characters. As Jordan (1898) noted, ". . . we have here an instructive illustration of the fact—so very often entirely disregarded in classificatory work—that the presence of the same character in two different [taxa] . . . is, evidence of closer relationship only, if the character is a specialisation and not of the ancestral type." Jordan's logic is simple, but has been largely ignored by butterfly systematists.

The application of stability and monophyly to groups with an established generic nomenclature, such as the bulk of the butterflies, is straightforward. If a genus is monophyletic, do not change the name. If a genus is not monophyletic, choose the combination of monophyletic generic groupings that will create the fewest name changes. If another option causes more name changes now but will be more stable in the future because of better evidence for monophyly, then present the reasons and evidence for that choice.

Ehrlich and Murphy (1982) suggested that the concept of balance

(the equivalence of categorical rank in related taxa, *sensu* Mayr 1969) also be used to decide generic nomenclature. Despite Mayr's discussion of how balance might be applied, this method is subjective, particularly since it is unclear exactly what the method is supposed to estimate. Although objectivity is not itself justification for using a criterion, we believe that an obviously subjective one, such as balance, will promote instability of butterfly generic nomenclature.

Kudrna (1974) and Higgins (1975) used the criterion of "similarities and differences" to justify their recognition of *Artogeia*, and did not mention stability and monophyly. For example, Higgins (1975) stated, "Their [*Artogeia*] genitalia, androconial scales and chromosome numbers differ from those of *P. brassicae* and it is not satisfactory to include them in the same genus." Neither worker suggested that *Pieris*, as used by Klots (1933) or Bernardi (1947), was polyphyletic. Neither discussed the possible confusion that would result from changing the generic nomenclature of *P. rapae* and *P. napi*.

There are many problems with the criterion of similarities and differences. (1) The similarities and differences used by Kudrna and Higgins do not provide information on the phylogenetic position of *P. rapae*. This example is a clear illustration that similarities and differences alone are insufficient to establish monophyly. (2) If Kudrna and Higgins had examined female genitalia and isozymes (as opposed to male genitalia, androconia, and chromosome numbers), they would have put *rapae* in *Pieris*. When taxonomic conclusions depend upon the character set used, the result is instability. (3) We are certain that Kudrna and Higgins believed that *Artogeia* should be split from *Pieris* because it is "sufficiently different." However, if one "authority" states that a difference is sufficient to split a genus, but another disagrees, then how can these conflicting views be resolved? It is evident that the criterion of similarities and differences promotes instability, and should not be used.

Kudrna (1974) and Higgins (1975) assumed that the divergent morphology of *P. brassicae* is the result of phylogenetic distance, but did not consider that it might be the result of rapid evolution. We hypothesize that rearrangement of genes caused by extensive chromosomal fusion—haploid chromosome number decreased from about 26 to 15 at point C in Figs. 1 and 2 (discussion in White 1973)—affected gene expression during development (the "position effect"; Dobzhansky 1957, White 1973), and is causally related to the divergent male genital, androconial, and larval (D. Weisman, pers. comm.) morphology of *P. brassicae*. Chromosomal rearrangements would not be expected to affect the protein products of structural genes, however—an expectation consistent with isozyme data (Geiger 1981, Geiger & Scholl 1985). Our

hypothesis generates the testable prediction that morphology and chromosome numbers are perfectly correlated; all species in the *P. brassicae* group should have reduced haploid chromosome numbers (about 15) while none in the *P. rapae* and *P. napi* groups should have the reduced numbers.

· J. H. Comstock (1893) wrote: "Here I believe lies the work of the systematist of the future. The description of a new species, genus, family or order, will be considered incomplete until its phylogeny has been determined so far as is possible with the data at hand." Comstock's vision of the holarctic butterfly "systematist of the future" is, by and large, still just a vision. Until we have reasonable phylogenies, generic nomenclature is bound to be unstable. In the meantime, suggested changes in generic nomenclature will hopefully be based on evidence of monophyly, and proposed with due regard for stability.

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RESTINGA BUTTERFLIES: BIOLOGY OF
SYNARGIS BRENNUS (STICHEL) (RIODINIDAE)

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ABSTRACT. *Synargis brennus* (Stichel) is a myrmecophilous riodinine butterfly that inhabits the restinga, a low forest on the Brazilian coast. The larval food plant *Dalbergia ecastophylla* has nectaries attractive to ants of the genera *Camponotus* and *Azteca*. Ants attend the larvae, drumming on them to stimulate a secretion which they subsequently eat from two glands located on the eighth abdominal segment.

This paper continues the series of studies on restinga butterflies started with the biology of *Menander felsina* (Callaghan 1977). The urgency of the study of this habitat is underlined by the fact that the site of the latter study near Rio de Janeiro has been destroyed by a housing development.

Synargis brennus (Stichel) (Fig. 1), a myrmecophilous riodinine butterfly, is not an endemic restinga species, but is found mostly in this habitat, and forms an important element of its fauna. The butterfly ranges from the coast in southeast Brazil across the Planalto to the Amazon basin, where it intergrades with *S. calyce* (Felder). The habitat where the observations were made is called "restinga", and consists of low, scrubby, dense, woody vegetation growing along the coast. The vegetation and physical characteristics are summarized in Callaghan (1977). The observations in the present study were made over three months during visits to Buzios, a very dry section of coastline 170 km E of Rio de Janeiro (Fig. 2).

Observations were made in the field and in the laboratory. The letters T and A followed by a number refer to thoracic and abdominal segments, respectively.

DESCRIPTION OF IMMATURE STAGES

Egg (Fig. 3). Rounded laterally, flattened dorsally and ventrally, giving the appearance of a fat tire. Color shiny bronze, with a network of small ribs forming a hexagonal pattern smaller around the micropyle and ventrally; top of ribs irregular, with a small tubercle at each intersection. Micropyle circular, depressed, with numerous small openings. Duration 9 days (N = 5).

First instar. Length 1.8 mm, head width 0.2 mm. Form rounded dorsally, flat ventrally. Head black, numerous small setae on face. Thorax light brown with black dots, pair of reddish, broken lines dorsally; T1 bilobed, with eight long cilia pointed cephalad, a spiracle on each side. T2 and T3 with three long setae laterally at base of tergum. Abdomen with pair of reddish lines dorsally. Four lateral setae on each segment except last, on which there are six long setae pointed caudad. Spiracles on segments A1–A8, indistinct; those on A1 located ventrally, those on A2–A8 laterally. Duration 6 days (N = 5).

FIGS. 1–9. **1,** Female *Synargis brennus* resting between ovipositions; **2,** Study site in restinga woods, Buzios, Rio de Janeiro, Brazil; **3,** Egg shells on stem of foodplant; **4,** Second instar attended by a *Camponotus* ant; **5,** Ants tending third instars on host plant; **6,** Fourth instars; **7,** Ant tending fifth instar; **8,** Prepupa; **9,** Pupa.

Second instar (Fig. 4). Length 4 mm, head width 0.4 mm. T1 light brown with two black horns pointed cephalad, bearing two setae extending from the ends, and many small teeth on the surface; between the horns cephalad are two vibrating papillae; below each horn is a lateral scolus with two long setae. T2 and T3 with two major lateral setae each. A1–A9 with four lateral setae on edge of tergum; A9 and A10 with tail plate and six long setae pointed caudad. All setae with numerous small spines. A8 with Newcomer's organs well developed as two raised slits. Duration 5 days (N = 9).

Third instar (Fig. 5). Length 6 mm, head width 0.9 mm. Head black, thorax and abdomen light green dorsally, light yellow ventrally. Horns of prothorax black; anal plate light brown, tegument covered with small white points. Spiracles light brown. Duration 6 days (N = 7).

Fourth instar (Fig. 6). Length 10 mm, head width 1.2 mm. Like third instar, except area between horns on prothorax and cephalad of anal plate dark brown. Duration 5 days (N = 4).

Fifth instar (Fig. 7). Length 15–19 mm, head width 1.7 mm. Like fourth instar except T2 and T3 with V-shaped figure dorsally pointed caudad; A8 with light brown saddle between the Newcomer's organs. Duration 7 days (N = 3).

Prepupa (Fig. 8). Length 19 mm. Like fifth instar except integument mottled brown-gray, white spiracles. Duration 3 days (N = 2).

Pupa (Fig. 9). Length 15 mm, width at widest part 5 mm. Two rounded horns cephalad with T-shaped black spot behind them; thoracic segments with dorsal hump; abdominal segments wide, flat dorsally, first two widest, terminating laterally in a scolus with spiracle surrounded by spoon-shaped scales, two rows of similar scoli located dorsally, two to each segment. Pupa secured by cremaster and silk girdles. Color mottled gray-brown to greenish, varying in pattern between individuals. Duration 11 days (N = 2).

Preserved material is in the author's collection. Larvae of *S. brennus* are similar to those of *Juditha molpe*. The latter differs in being lighter green with yellow dots dorsally, and in the smooth face and horns. Otherwise, the larvae are morphologically very close. The ventrally positioned spiracle on A1 is the same in both. This suggests that *S. brennus* and *J. molpe* may be congeneric.

BIOLOGY

The foodplant of *Synargis brennus* is *Dalbergia ecastophylla* (Linn. & Talb) which is common throughout the restinga. The leaves are simple, ovate, and alternate along a woody stem, with a nectary at the base of each petiole. The plant grows as a vine, winding its way through the branches of other trees and shrubs, making the restinga all but impenetrable.

Females oviposit during the afternoon on all parts of the foodplant: leaves, leaflets, petiole, stem at base of petiole, nectaries. They first feel the surface with the tip of the abdomen. The egg is laid quickly, in less than one minute (N = 5), the female then flying to another nearby leaf where she rests for a few minutes before returning to another part of the foodplant to oviposit again. The eggs were placed near *Camponotus* ants, which surrounded the female but were not hostile.

Newly hatched larvae fed on new leaf buds or at the nectaries, and these preferences were maintained throughout larval development. As the nectaries dried up, and the leaves became tough and leathery, the larvae aggregated on new plant growth. Feeding took place mainly at night, the larvae remaining motionless on leaves or stem during the day where cryptic coloration made them difficult to locate. They spent their time exclusively on the foodplant, resting or moving about, weaving the head from side to side as they laid down silk by which they secured their grip. When disturbed, they raised the front half of the body, flopping it about.

From the second instar on, larvae were attended by ants (Figs. 4, 5, 7), either *Camponotus crassus* ssp., which also attends *M. felsina* larvae in the restinga (Callaghan 1977), or *Azteca* sp. I never found the two species of ants together on the same plant. The ants drum their antennae on the larval head and thorax, thereby stimulating secretion of honeydew by Newcomer's organs. The ants then consumed the secretion. As with *M. felsina* and *J. molpe, Camponotus* ants protected the larvae by spraying formic acid at intruders (Callaghan 1982). The larvae possess vibratory papillae; these vibrate rapidly when they walk, and may attract ants.

Larvae with no or few ants were sometimes parasitized. I discovered one solitary, unattended larva parasitized by an ichneumon wasp. The larvae are not otherwise dependent on ants. In the laboratory, I raised larvae from first instar to pupation without ant presence.

Like *J. molpe, S. brennus* larvae are cannibalistic. On two occasions, when fresh food was lacking in the laboratory, the larger *brennus* larvae killed and ate smaller ones. This behavior in nature increases the chances of later instar larvae reaching pupation, should food resources fail.

At the end of the fifth instar, larvae turn a mottled brown-gray, cease feeding, and remain motionless on the foodplant. Pupation takes place on the ventral surface of the leaves, and the ants lose interest. The imago emerges 11 days later.

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MALE AND FEMALE GENITALIA OF *PHOEBIS EDITHA* (BUTLER): HOW THEY DIFFER FROM HISPANIOLAN *P. SENNAE* (LINNAEUS) (PIERIDAE)

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ABSTRACT. Male and female genitalia of the Hispaniolan endemic *Phoebis editha* are figured, described, and compared with those of superficially similar *P. sennae* from Hispaniola. Results are based on 14 male and 2 female *P. editha,* and 17 male and 2 female *P. sennae.* Males of *P. editha* differed from those of *P. sennae* in at least six ways, including narrower sacculus, and longer ampullary process. Females of *P. editha* differed from those of *P. sennae* in at least five ways, including more heavily sclerotized apophyses anteriores, and shorter, wider 8th tergum. These differences, together with the facts of sympatry, synchronism, and different larval foodplants, suggest that the taxa are specifically distinct and not forms of the same species.

Phoebis editha, endemic to Hispaniola, was originally described as a distinct species (Butler 1870). Due to superficial similarity between the males of *P. editha* and *P. sennae,* the taxonomic status of the former has been in doubt. Most recently, D'Abrera (1981) suggested *P. editha* may represent a rare form of *P. sennae.* The female of *P. editha* at times has been considered a dry season form of *P. sennae,* or even of *P. philea* (Johansson). This latter view is reported, but not endorsed, by Riley (1975).

Recently, I stated reasons why *P. editha* should be considered specifically distinct from *P. sennae,* the most important of which were sympatry, synchronism, different larval foodplants, and different male genitalia (Coutsis 1983). Due to unavailability of material at the time, I was unable to illustrate the genital differences.

It is now possible for me to describe and figure male and female genitalia of *P. editha* because I have been able to borrow two male and two female specimens. For comparison, genitalia of two male and two female Hispaniolan *P. sennae* are also figured. The findings agree with those derived from a study of 12 male *P. editha* and 15 male *P. sennae,* which I carried out between 1952 and 1958 while doing field work in Hispaniola.

The drawings were done using a Wild M5 stereomicroscope with drawing tube. The appendages were studied and drawn while they were immersed in 80% ethyl alcohol, free from pressure due to slide mounting, and thus free from distortion.

The genital terminology used is based on Tuxen (1970) and Higgins (1975).
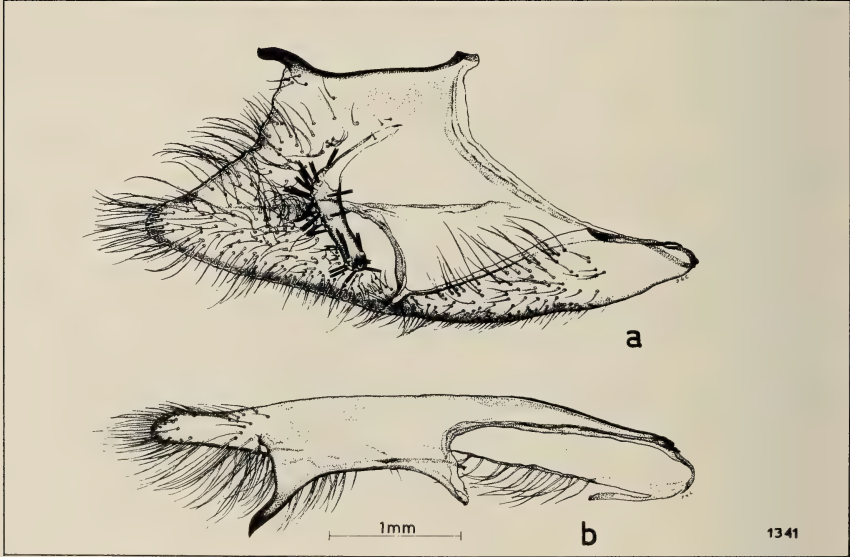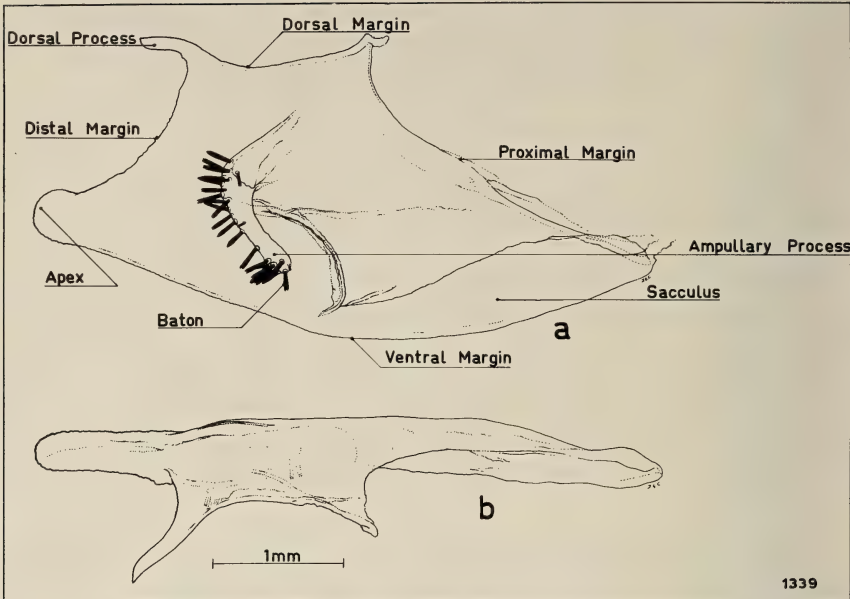
FIG. 1.   Male *Phoebis editha* from Port-au-Prince, Haiti. (a) Lateral view of interior face of left valva; (b) Dorsal view of left valva. Top: Line drawing, prep. 1339, coll. 9 July 1955. Bottom: Shade drawing, prep. 1341, coll. 13 July 1955.
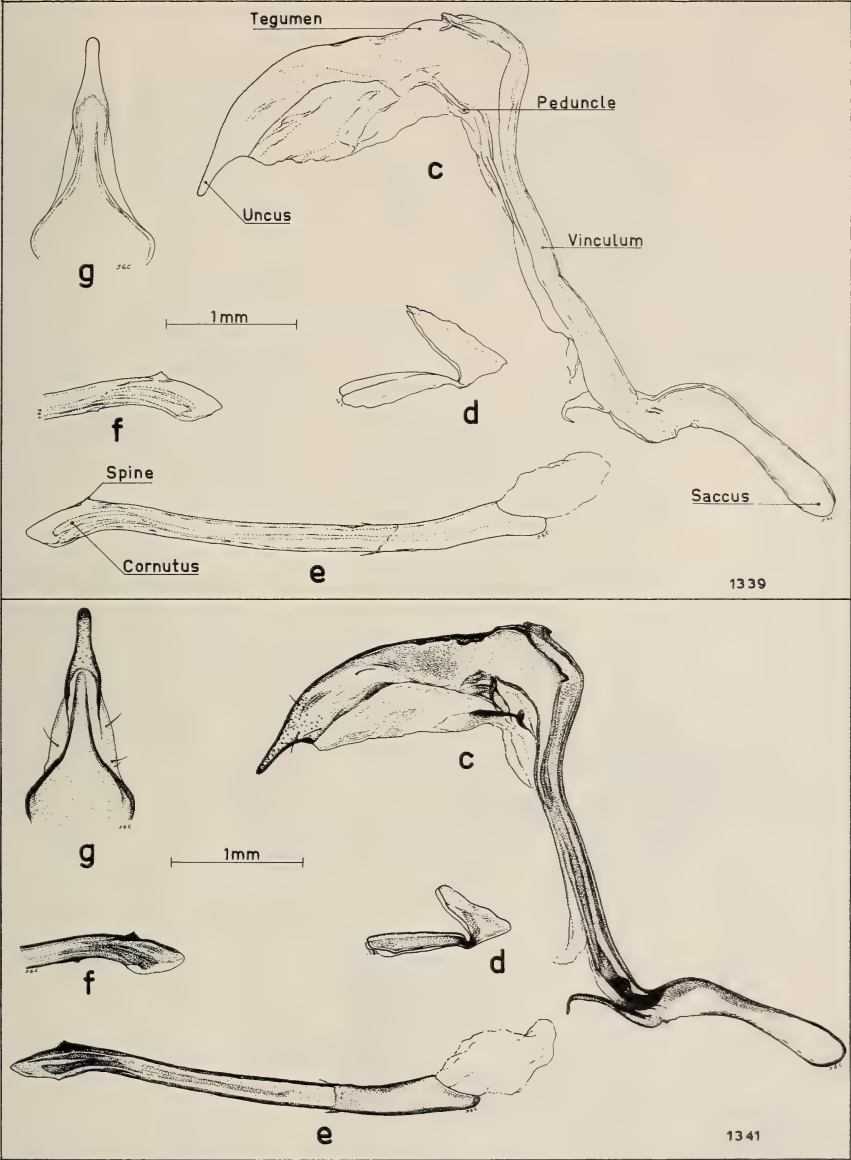
FIG. 2.   Male *Phoebis editha* from Port-au-Prince, Haiti. (c) Lateral view of right side of genitalia (valvae, aedeagus, furca removed); (d) Lateral view of right side of furca; (e) Lateral view of right side of aedeagus; (f) Dorsolateral view of left side of distal end of aedeagus; (g) Dorsal view of uncus and tegumen. Top: Line drawing, prep. 1339. Bottom: Shade drawing, prep. 1341.

TABLE 1.　Differences between male genitalia of *P. editha* and *P. sennae*.

Species	Dorsal margin of valva	Sacculus	Ampullary process	Apex of valva	Dorsal process of valva	Uncus
P. editha	Shorter than distal margin of valva	Narrower than in *P. sennae*	Twice as long as in *P. sennae*	Rounded, simple	Cylindrical, with pointed distal end. One-half as wide as in *P. sennae*	Distal end bulbous in dorsal view
P. sennae	Longer than distal margin of valva	Wider than in *P. editha*	One-half as long as in *P. editha*	Complex, with pointed extension	Flat, tapering to a point. Twice as wide as in *P. editha*	Distal end not bulbous in dorsal view

TABLE 2.　Differences between female genitalia of *P. editha* and *P. sennae*.

Species	Signum	8th tergum	Apophysis anterior of 8th tergum	Ring formed by 8th tergum and lamella antevaginalis	Ventral lobe of papillae anales
P. editha	Distal edge evenly curved	Shorter, but wider than in *P. sennae*	More heavily sclerotized than in *P. sennae*	Of greater diameter than in *P. sennae*	Almost twice as long as in *P. sennae*
P. sennae	Distal edge unevenly curved and with pointed projection	Longer, but narrower than in *P. editha*	More lightly sclerotized than in *P. editha*	Of lesser diameter than in *P. editha*	Slightly more than half as long as in *P. editha*

FIG. 3. Female *Phoebis editha* from Port-au-Prince, Haiti. (h) Dorsal view of genitalia; (i) Lateral view of left side of genitalia (corpus bursae, ductus bursae, appendix bursae omitted). Top: Line drawing, prep. 1603, coll. 27 July 1955. Bottom: Shade drawing, prep. 1604, coll. 2 July 1954.
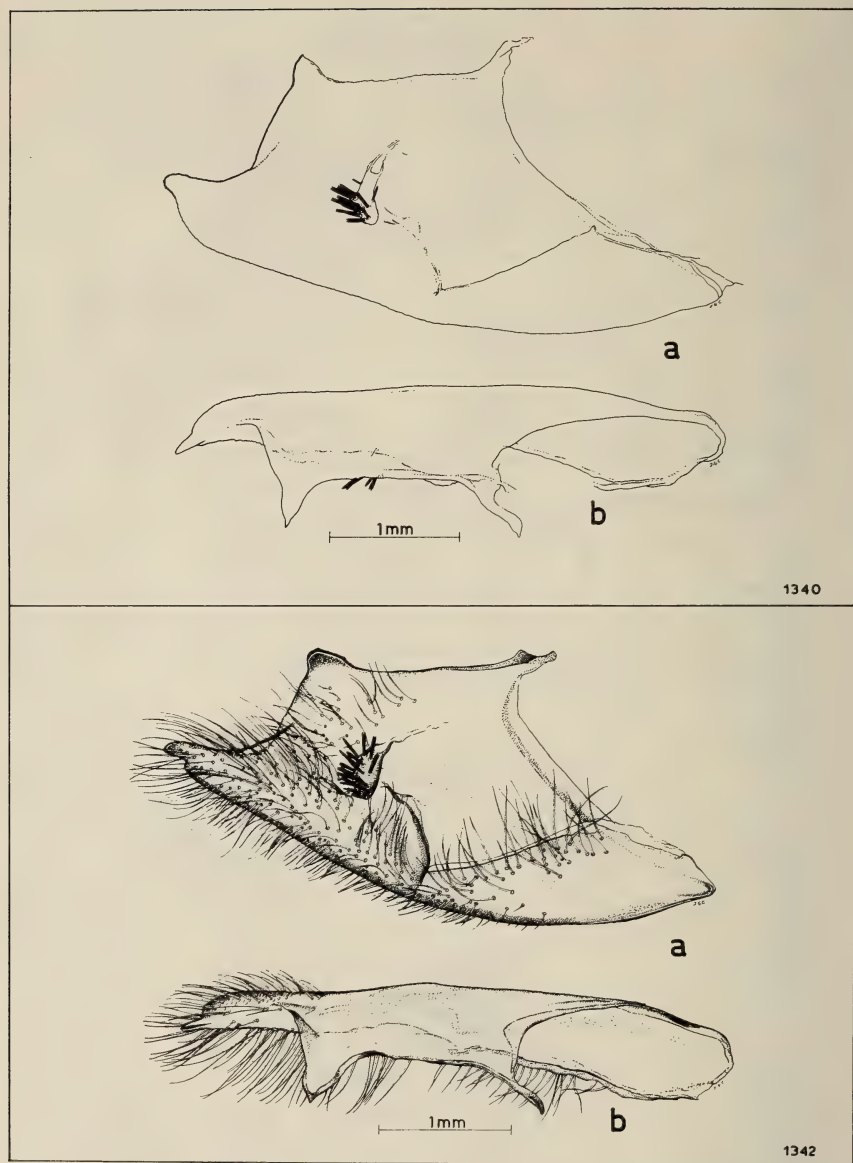
FIG. 4.   Male *Phoebis sennae* from Haiti. (a) Lateral view of interior face of left valva; (b) Dorsal view of left valva. Top: Line drawing, prep. 1340, coll. Gros Morne, 2 July 1954. Bottom: Shade drawing, prep. 1342, coll. Port-au-Prince, 13 July 1955.
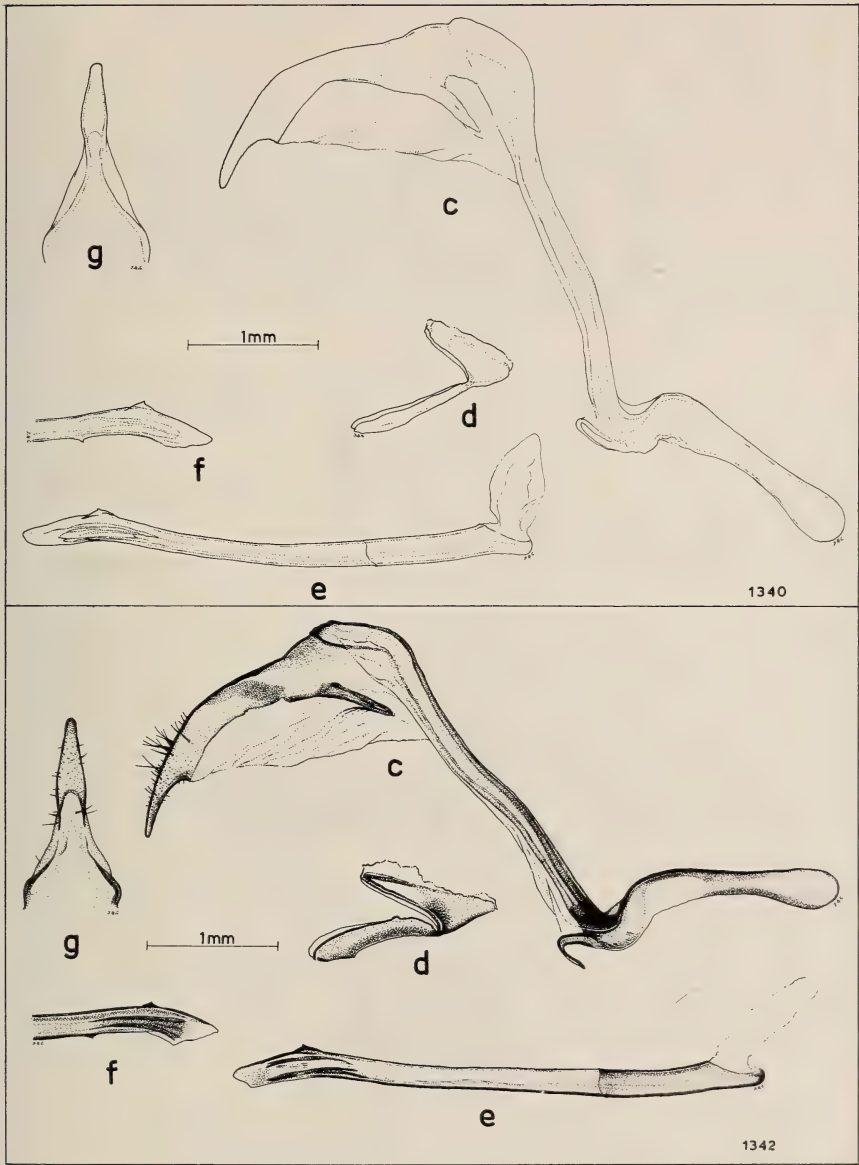
FIG. 5. Male *Phoebis sennae* from Haiti. (c) Lateral view of right side of male genitalia (valvae, aedeagus, furca removed); (d) Lateral view of right side of furca; (e) Lateral view of right side of aedeagus; (f) Dorsolateral view of left side of distal end of aedeagus; (g) Dorsal view of uncus and tegumen. Top: Line drawing, prep. 1340. Bottom: Shade drawing, prep. 1342.
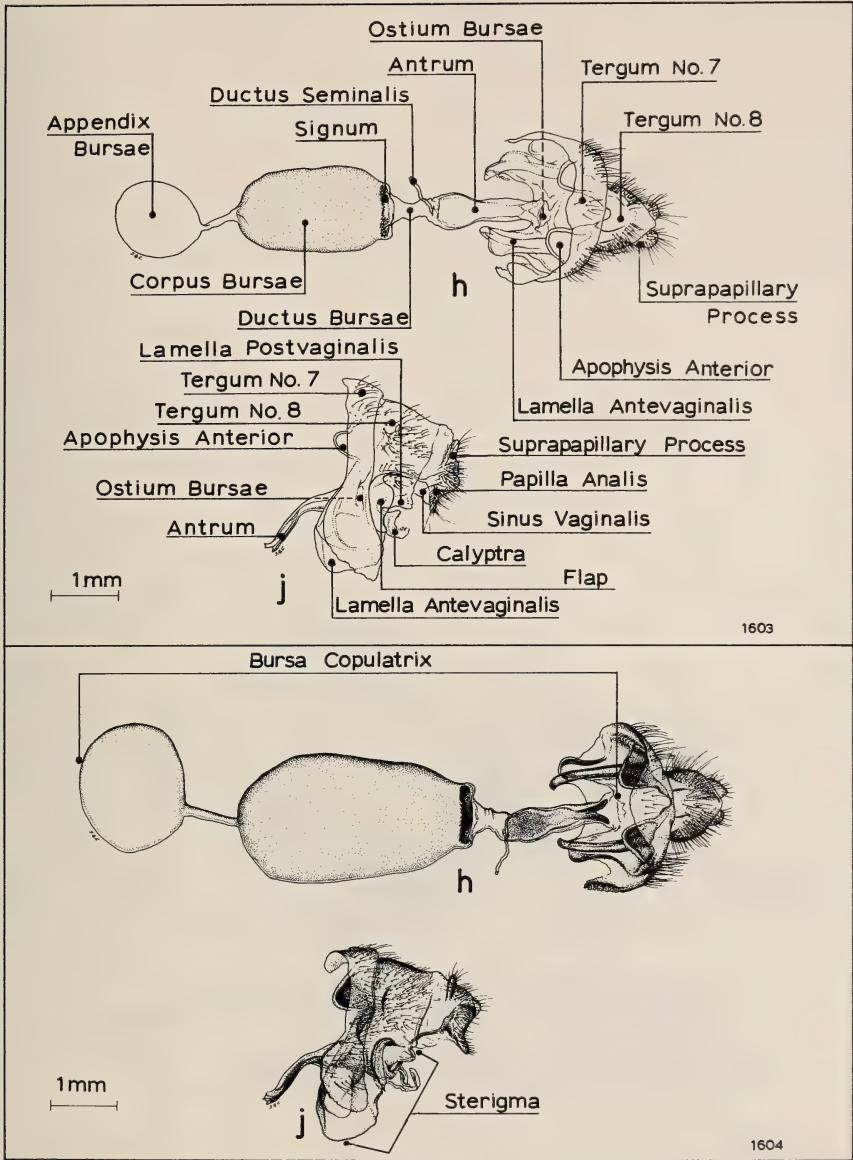
FIG. 6.   Female *Phoebis sennae* from Haiti. (h) Dorsal view of genitalia; (i) Lateral view of left side of genitalia (corpus bursae, ductus bursae, appendix bursae omitted). Top: Line drawing, prep. 1605, coll. Gros Morne, 4 July 1954. Bottom: Shade drawing, prep. 1606, coll. Port-au-Prince, 13 July 1955.
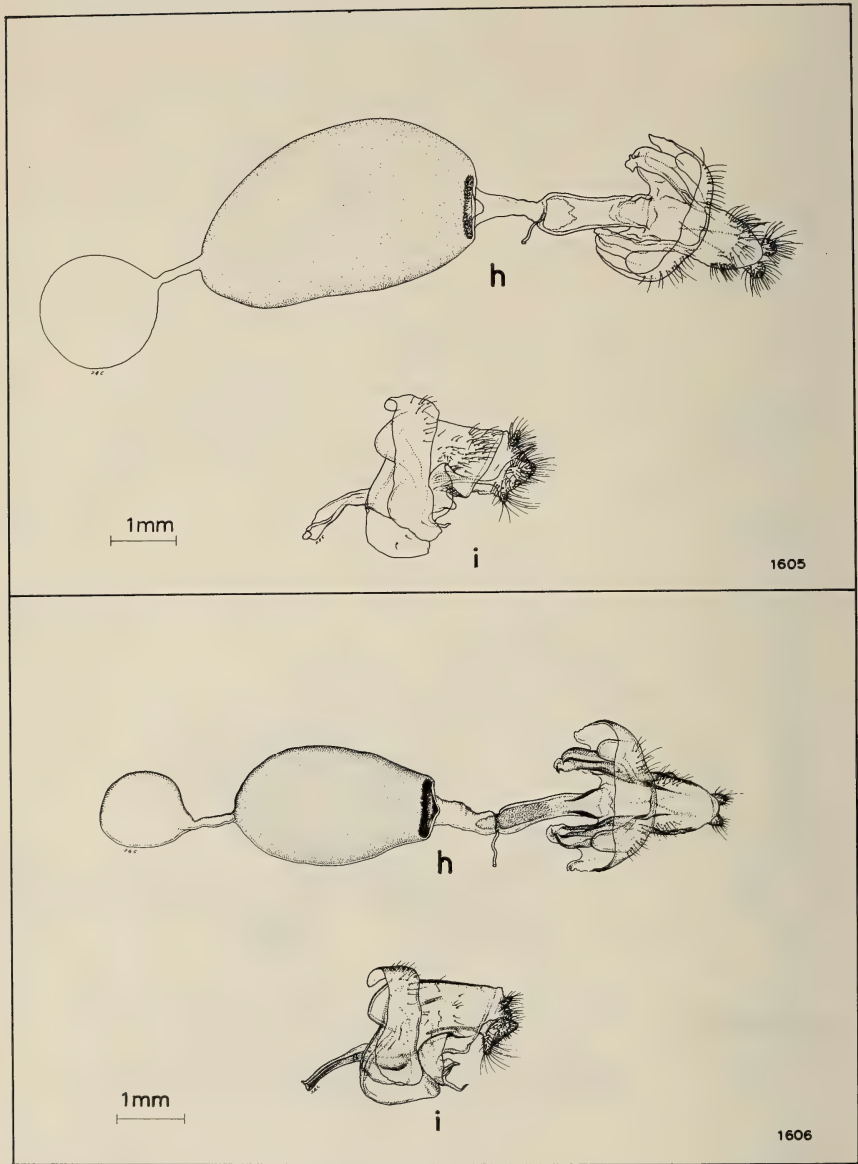
DESCRIPTION OF *PHOEBIS EDITHA* GENITALIA

Male genitalia (Figs. 1 & 2). Valva flat; dorsal, proximal and distal margins concave; ventral margin convex; dorsal margin shorter than distal margin; distal margin about ⅓ length of ventral margin. Sacculus well defined, greatest width about ¼ total length. Ampullary process cylindrical, sclerotized, gently curved toward proximal margin of valva, possessing a rounded apex, and covered with heavily sclerotized, stiff, cylindrical batons with bifurcate distal ends; overall length of ampullary process about ⅔ that of dorsal margin of valva. Apex of valva rounded; junction between dorsal and distal margins of valva possessing a cylindrical, inward directed, heavily sclerotized dorsal process, about ½ length of dorsal margin of valva, with pointed distal end.

Uncus fused with tegumen, without visible suture, possessing no definable proximal edge; distal part of uncus in lateral view tapering to a rounded point; uncus in dorsal view 1½ times as wide as in lateral view, possessing blunt and imperceptibly bulbous apex.

Tegumen forming shallow dome; peduncles poorly defined. Vinculum in lateral view about same length as combined length of tegumen and uncus.

Saccus about ⅔ as long as combined length of tegumen and uncus, bent downward, with rounded distal end.

Furca composed of two dorsal and two ventral processes, latter about ½ as wide and 1⅓ times as long as former.

Aedeagus about 1½ times as long as combined length of tegumen and uncus, bent upward along basal ¾, downward along distal ¼, possessing a single dorsal, flat spine near distal end, and a single ventrolateral flat spine basad of dorsal spine on left side, resulting in an asymmetrical arrangement; vesica with two oblong, sclerotized cornuti near distal end of aedeagus.

Female genitalia (Fig. 3). Corpus bursae membranous, diaphanous, oblong, flask-shaped and expansible (thus of varying size); surface of membrane possessing numerous minute excrescences in the form of dots; a single oblong signum present near junction with ductus bursae; signum perpendicular to longitudinal axis of corpus bursae; dorsal and proximal part of signum possessing numerous spines.

Appendix bursae likewise diaphanous and membranous, devoid of excrescences, spherical in shape; connected to corpus bursae by a diaphanous tube.

Ductus bursae tubular, diaphanous; antrum sclerotized and about three times as long as ductus bursae; ductus seminalis arising dorsally from junction between ductus bursae and antrum.

Lamella antevaginalis massive, sclerotized, shaped like a locomotive "cow catcher"; laterally fused with 8th tergum, forming with it a complete, uninterrupted ring with no visible suture; lamella postvaginalis with a movable protuberance, the calyptra, composed of lightly sclerotized and intricately folded membranes, blocking ostium bursae; ostium bursae laterally flanked by two free-standing membranous flaps.

Apophyses anteriores of 8th tergum sclerotized; papillae anales bilobed; ventral lobe about half as wide as dorsal, but equal in length to it; dorsum of membranous area between 8th tergum and papillae anales with rounded, lightly sclerotized suprapapillary processes.

DIFFERENCES BETWEEN GENITALIA OF
PHOEBIS EDITHA AND *PHOEBIS SENNAE*

Male genitalia (Figs. 1, 2, 4, 5). The differences are summarized in Table 1.
Female genitalia (Figs. 3, 6). The differences are summarized in Table 2.

The structural differences between *P. editha* and *P. sennae*, together with the fact that these butterflies are sympatric, synchronous, and have different larval foodplants, show that these taxa are specifically

distinct, and not, as some authors have suggested, forms of the same species.

ACKNOWLEDGMENT

I thank C. L. Remington for allowing me to borrow and dissect the genitalia described and figured here.

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GENERAL NOTE

SMALL–NICOLAY COLLECTION TO SMITHSONIAN

The National Museum of Natural History (Smithsonian Institution) is receiving the G. B. Small, Jr.–Col. S. S. Nicolay Collection of New World Butterflies. The scientific value of the collection is inestimable. It contains more than 3,800 species including about 450 undescribed taxa. Its representation and identification of New World Hesperiidae, Lycaenidae, and Riodinidae are now better than that in most museums. Coverage of Panama is approximately 98% complete, making its butterfly fauna better known than that of any other continental neotropical country. Geographically variable species, particularly from Panama, are represented by long series from many localities. Because so much neotropical forest has been destroyed, many of these specimens represent a unique record of the original fauna. Besides Panama, the collection is rich in material from Brazil, Costa Rica, Ecuador, Peru, and the United States.

The Small–Nicolay Collection contains 98,500 specimens, of which more than 42,500 are spread. There are 237 paratypes.

Lepidopterists who expect to be in the Washington, D.C., area may visit the Smithsonian and examine the collection by prearrangement.

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GENUS *DIPTYCHOPHORA* ZELLER AND A RELATED NEW GENUS *STENEROMENE* FROM THE NEOTROPICAL REGION (PYRALIDAE: CRAMBINAE)

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ABSTRACT. *Diptychophora* Zeller a Neotropical–southern Nearctic fringe genus of the subfamily Crambinae, is redefined. The type species *D. kuhlweini* Zeller, presently a junior synonym of *D. azanalis* (Walker), is resurrected and shown to be distinct. *Diptychophora diasticta* is described as new, *D. subazanalis* Błeszynski is elevated to specific rank, and *Mysticomima desmoteria* Meyrick is transferred to *Diptychophora* from its present position in Pyraustinae. *Diptychophora azanalis* is transferred, along with *Pareromene nymphocharis* (Meyrick), to the new genus *Steneromene* which is defined and distinguished from *Diptychophora*.

The genus *Diptychophora* Zeller (Pyralidae: Crambinae: Diptychophorini) originally contained a single species from Brazil, *D. kuhlweini* Zeller, but subsequently became a repository for scores of small Crambinae from all over the world except the northern Holarctic (Meyrick 1931–33, Błeszynski & Collins 1962). Błeszynski (1965) determined that *Pareromene* Osthelder, erected for one species, *P. rebeli*, from Crete was the appropriate genus for all Old World "*Diptychophora*", and this name has since been used for these insects (Błeszynski 1966, 1970, Gaskin 1971, 1974a, 1974b, 1975). However, there are problems relating to the continued use of this name (Gaskin 1985). Błeszynski (1967) formally redefined *Diptychophora* Zeller as an exclusively neotropical-southern Nearctic fringe genus with four species and one subspecies, but this is unsatisfactory for several reasons. His "subspecies" *subazanalis* deserves full specific rank within *Diptychophora* while *azanalis* requires a new genus to exclude it from *Diptychophora*. Błeszynski also transferred the balance of named New World forms (then totalling nine species) to *Pareromene*. The status of these will be examined elsewhere.

During a long-term revision of the Diptychophorini of the world, all the above material was re-examined by the author and Michael Shaffer of the British Museum (Natural History), together with new finds from several collections not seen by Błeszynski. The purpose of the present paper is to redefine the genus *Diptychophora*, since the diagnosis given by Błeszynski (1967), essentially in three lines, is inadequate; to resurrect the type species *D. kuhlweini* Zeller, since it is not synonymous with *D. azanalis* (Walker) as indicated by Błeszynski and Collins (1962) and Błeszynski (1967); to transfer one species described in Pyraustinae to *Diptychophora*; to describe a new species of

the genus from Brazil; and to define a new genus *Steneromene* to contain *D. azanalis* (Walker) and *Pareromene nymphocharis* (Meyrick).

The following abbreviations for institutions are used in the text: BMNH (British Museum (Natural History)); CNIC (Canadian National Insect Collection, Ottawa); UMO (University Museum, Oxford, UK); USNM (United States National Museum of Natural History). In descriptions of male genitalia the LMB ratio refers to the length–median breadth ratio of the aedeagus. Decimals indicate the position of features, as a proportion of the total length of a structure or organ. In the forewing, measurements along the costa are taken from the base, those along the termen/margin from the apex, and those along fascia from the costa. In the male genitalia, measurements along the uncus, gnathos, valva, valval costa and aedeagus are from the base of each. In the female genitalia, measurements along the ductus bursae are made from the ostium.

Diptychophora Zeller

Diptychophora Zeller (1866). Type species *Diptychophora kuhlweini* Zeller (1866) (by monotypy).
Scissolia Barnes & McDunnough (1914). Type species *Scissolia harlequinalis* Barnes & McDunnough (1914) (by monotypy) [Syn. Błeszynski 1967].
Colimea Dyar (1925). Type species *Colimea incisalis* Dyar (1925) (by monotypy) [Syn. Błeszynski 1967].
Mysticomima Meyrick (1931). Type species *Mysticomima desmoteria* Meyrick (1931) (by monotypy) [New synonymy (from Pyraustinae)].

Revised description. In forewings, Sc and R_1 concurrent, R_3 vestigial or absent. In hindwings, M_3, Cu_1 arising from common stalk, or individually from distal margin of hindwing cell. Male genitalia with characteristic "fish hook" gnathos, tubular, tapered to apex, hooking occurring at junction of basal elements. Saccus almost vestigial, juxta simple. Setulose valva highly modified, secondarily simplified, in most species broader than long, terminating distally in dorsal and ventral blunt lobes. Female genitalia simple: Antrum usually broad, membranous, ductus bursae also broad with or without subantral expansion. Corpus bursae bearing scobinate patch or distinct signum, usually crescentic.

Key to Species of *Diptychophora*

1 ♂: Sclerotized anellar structure present around aedeagus. [Female not known] .... *diasticta*
– Sclerotized anellar structure absent 2
2(1) ♂: Ventral margin of valva slightly rounded, but with saccular region not developed into distinct lobe. ♀: Ductus bursae with secondary swelling anterior to corpus bursae ..... *kuhlweini*
– ♂: Ventral margin of valva terminating in a distinct projecting, saccular lobe. ♀: Ductus bursae without secondary swelling anterior to corpus bursae 3

3(2) ♂: Vinculum broad, half as wide as length of uncus; gnathos tapered to smoothly pointed apex. ♀: Antrum a membranous funnel, wider than length of 8th abdominal tergum; corpus bursae with broad, diffuse scobinate patch, no distinct signum .... *subazanalis*

— ♂: Vinculum a narrow strip at base of valva: gnathos tapered abruptly, hooked dorsad. ♀: Antrum a membranous funnel if flared, considerably narrower than length of 8th tergum; corpus bursae with distinct signum 4

4(3) ♀: Ductus bursae lacking flared antrum, latter slightly "crimped"; 7th sternum with tapered and rounded posterior margin. [Male not known] .... *incisalis*

— ♂: as described in 3–. ♀: Antrum of ductus bursae flared at entrance; 7th sternum not tapered and barely rounded posteriorly 5

5(4) ♂: Costal lobe of valva relatively broad, length to width ratio about 2.2:1. ♀: Antrum of ductus bursae membranous, with smooth margin; corpus bursae with small, crescentic narrow, horizontal signum .... *desmoteria*

— ♂: Costal lobe of valva quite elongate, length to width ratio about 3.5:1. ♀: Antrum of ductus bursae with slightly crenulate margin, somewhat sclerotized; corpus bursae with large, tapered, horizontal signum with infolded lower (anterior) margin .... *harlequinalis*

Diptychophora diasticta, new species

Exterior description (Fig. 5). Alar expanse 12 mm (N = 1). Labial palpi, head, antennae brown, head with postcephalic, buff scale tuft. Thorax and abdomen brown with scattered darker scaling. Ground color of forewings creamy white, heavily irrorated with brown clouding. Basal fascia obsolete, position marked with scattered brown scales. Antemedial fascia cream, zigzagged, broad, thickly bordered with dark brown. Discal region clouded with brown, cream zone just distal of median transverse line. Costa with orange area at about 0.7 and small oblique central white bar. Postmedial fascia wider toward dorsum, also becoming less distinct, zigzagged from 0.5, with thick dark brown margins. Terminal zone cream, heavily clouded with brown. Margin with stripe of bright orange from 0.4–0.8, and row of 4 black spots. Apical zone clearly delineated by narrow white line extending from 0.8 of costa to subapical identation on termen, orange brown proximally, white distally, wedge of yellow scales on costal extremity. Cilia brown with darker brown apices. Hindwings dark brown. Ventral surfaces dark brown, apical and terminal markings repeated from dorsal surface.

Male genitalia (Fig. 9) (N = 1). Uncus simple, broad, spatulate, apically rounded, slight subapical constriction. Gnathos triangular in cross section, slightly tapered to apex, angled sharply dorsad at about 0.4. Tegumen simple, vinculum a strip at base of valva, saccus small, pyramidal. Juxta an elongate, apically tapered plate; hooked, double transtillalike structure present above juxta. Valva about 2.2× length of uncus, half as broad as long, broad posteroventral lobe. Sacculus, costal region of valva undeveloped. Aedeagus tubular, truncate, curved slightly dorsad, huge relative to rest of genitalia, about 1.8×
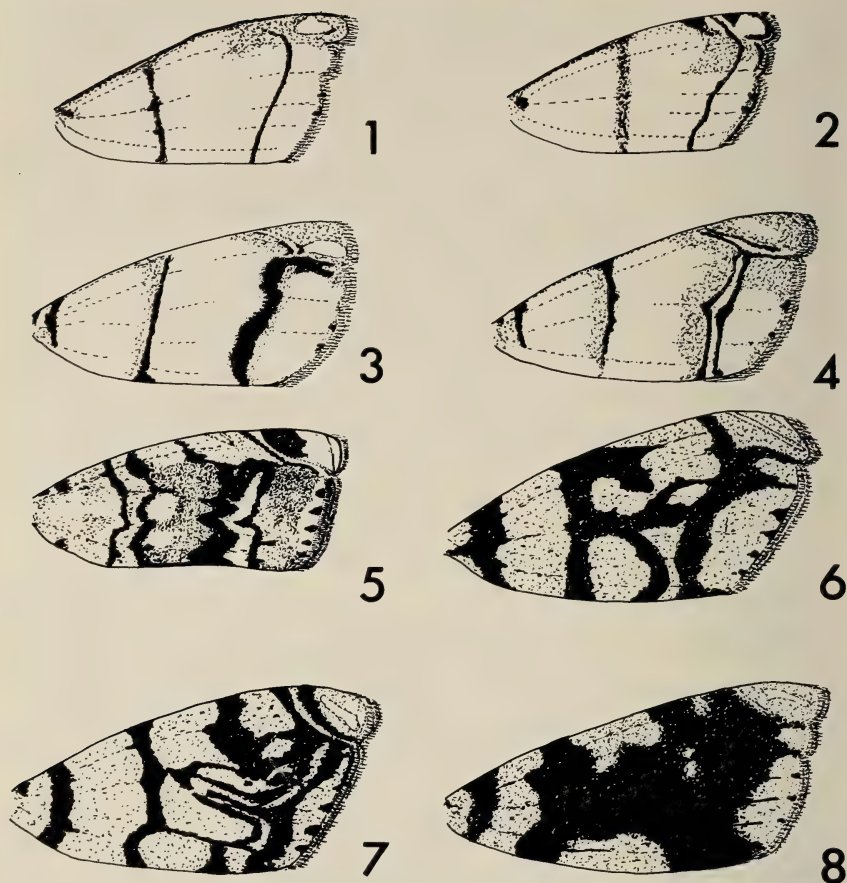
FIGS. 1–8. Forewings of *Steneromene* and *Diptychophora* species. **1,** *Steneromene azanalis*; **2,** *S. nymphocharis*; **3,** *Diptychophora kuhlweini*; **4,** *D. subazanalis*; **5,** *D. diasticta*; **6,** *D. desmoteria*; **7,** *D. harlequinalis*; **8,** *D. incisalis*.

length of valva. LMB ratio about 10:1, cornuti absent, scobinate patch of vesica in subapical region.

Type. Holotype ♂. Prov. de Bahia, Sao Antonia de Barra, Brazil, II.XII 1888, Gounelle, BMNH, genit. prep. Pyralidae 15351.

Discussion. Known only from the holotype, which is from eastern Brazil. Except for the development of a sclerotized, rather than membranous transtilla, the male genitalia are typical of the genus.

Diptychophora kuhlweini Zeller

Diptychophora kuhlweini Zeller (1866). [Holotype not located despite search of collections in Britain and Europe by author, M. Shaffer, and other curators.]

Diptychophora kuhlweini Zeller; Błeszynski & Collins (1962); Błeszynski (1967); erroneously synonymized with *D. azanalis* (Walker).

Exterior description (Fig. 3). Alar expanse 12 mm (N = 4). Labial palpi whitish, some dark scaling; head, thorax, largely dull white. Legs, straw; abdomen white, scattered dark scaling. Ground color of forewings shining white. Basal and antemedial fasciae nearly straight, proximally bright yellow ochre, distally blackish brown. Postmedial fascia proximally broad and blackish brown, distally broad and ochreous yellow. Subterminal line turning at right angles toward termen at about 0.2, touching margin at primary indentation of termen. Terminal zone white, a few yellowish scales near margin, two black spots at 0.6 & 0.7. Apical zone delimited by marginal indentation (a secondary indentation occurs at nearly 0.5) and by thin silvery white line running from costa at about 0.8 to angle of subterminal line, also joining with a weaker thin line angling proximally from the costa. Apical zone bright ochreous yellow, white wedge of scales at extremity, a horizontal, white, pendant-shaped mark above indentation. Hindwings shining white, few dark scales near apex.

Male genitalia (Fig. 10) (N = 3). Uncus broad, tapered, spatulate, apically rounded. Gnathos triangular in cross section, flat surface dorsad, sharply pointed, curved or angled very acutely dorsad at about 0.4. Tegumen simple, sclerotized bandlike margins. Vinculum a narrow strip at base of each valva. Saccus very small, juxta a weak, oval plate, almost membranous. Valva trapezoid in shape, basal length barely greater than dorsoventral width, dorsal margin about 1.8× width; dorsal margin sclerotized, apex tapering, rounded. Aedeagus small, barely 0.5× valva, tubular, apically truncate, LMB ratio about 5.5:1. Cornuti absent.

Female genitalia (Fig. 14) (N = 1). Anal papillae triangular, moderately sclerotized, weakly fused; 8th abdominal tergum narrow; anterior apophyses short, nearly as long as posterior apophyses; 7th abdominal sternum unmodified, slightly rounded posteriorly. Antrum weak, membranous, masked by margin of 7th sternum. Ductus bursae 6–7× length of posterior apophyses, membranous, flattened to about 0.5, where it is swollen and lightly reticulate. Corpus bursae with two crescentic signa.

Material examined. BRAZIL: 1 ♂, Castro, Parana, 950 m, Jones, no date BMNH, genit. prep. Pyral. 15353; 1 ♂, Petropolis, Prov. Rio de Janeiro, no date, BMNH, GS-5083-SB; 1 ♂, Nova Teutonia, –.X.1943, F. Plaumann, BMNH, Pyral. 16325; 1 ♀, Guaraquefaba, P.R., 7.XII.1970, V. O. Becker Collection, Brasilia, spec. no. 11,423.

Discussion. This species is probably widely distributed across the southern part of the Brazilian shield although its specific habitat is unknown. The flight period includes at least October and December.

Błeszynski (1967) noted that "too little of the typical *azanalis* material is available . . . to decide whether *subazanalis* is a distinct species or only a subspecies". It would appear that unknowingly, Błeszynski never examined any true *azanalis* material at all, since M. Shaffer and I were only able to locate the type and one other specimen, both in UMO. Had Błeszynski seen the genitalia of the type slide he would not have made the remark quoted above because congenerity is out of the question. M. Shaffer first drew my attention to inconsistencies in the forewing characters within the "*azanalis*" and "*subazanalis*" series accumulated by Błeszynski and stored at BMNH. When the specimens with the thicker, solid postmedial fascia angled beneath the apex were compared to the illustration of *kuhlweini* given by Zeller (1866), they matched exactly. We then compared the genitalia between specimens segregated on the basis of forewing pattern and again found consistent

differences, much more marked in the female than in the male (Figs. 9, 11, 14–16). We concluded that *kuhlweini* was a valid species of *Diptychophora*, and that synonymization with *azanalis* was invalid, and, furthermore, that *subazanalis* should be elevated to full specific rank within the genus. Both known specimens of true *azanalis* (Fig. 1) were also noted to differ consistently in forewing characters from *subazanalis* (Fig. 4), the postmedial fascia of the former being thin, single and curved towards the costal margin. The genitalia of both sexes of *azanalis* (Figs. 20, 22) are unlike those of any *Diptychophora*.

Diptychophora subazanalis Błeszynski, new status

Diptychophora azanalis subazanalis Błeszynski (1967). [♂ genitalia, mislabelled *D. examinalis subexaminalis*.]

Exterior description (Fig. 4). Alar expanse 8–12 mm (N = 23). Labial palpi, head, white with yellow, brown; thorax shining white, yellow lappets, chocolate brown shoulders. Ground color of forewings white. Basal and antemedial fascia broad, nearly straight, each proximally bright yellow, distally chocolate brown. Postmedial fascia narrow, composed of pair of slender dark brown parallel lines, angled sharply toward termen at about 0.2, angled again at about 0.6. In Peruvian specimens, second angle of inner transverse line sometimes detached as a dark brown blotch. A broad strip of bright yellow extends along proximal side of inner line. Apical zone bright ochreous yellow; a white streak curves through it from costa to termen. Terminal region filled anteriorly with yellow, posteriorly with white; margin bears two black spots at 0.5 and 0.7. Cilia brown with yellow clouding. Hindwings and their cilia shining white. Ventral surfaces brown on forewings, white on hindwings.

Male genitalia (Fig. 11) (N = 3). Uncus simple, broad, apically rounded, spatulate. Gnathos tubular, tapering sharply to point, curved acutely dorsad at about 0.4–0.5. Tegumen broad, divided into wide dorsal and ventral bands, juxta a simple oval plate, vinculum broad, half as wide in profile as length of uncus, saccus almost negligible. Valva characteristically wider than long, drawn into blunt, double apex dorsally and ventrally; costa of valva represented by thin sclerotized margin, sacculus undeveloped. Aedeagus short, tubular, apically truncate, LMB ratio about 6:1, cornuti absent.

Female genitalia (Figs. 15, 16) (N = 4). Anal papillae broad, slightly sclerotized marginally, relatively short posterior apophyses about 1.5× length of papillae; 8th abdominal tergum and anterior apophyses each about half length of posterior apophyses, 7th abdominal sternum unmodified. Antrum a very broad, shallow, basally constricted, weak funnel, ductus bursae otherwise broad, about 4.5× length of posterior apophyses. Ductus seminalis joining at about 0.4–0.5. Corpus bursae with huge, crescentic scobinate area or diffuse signum.

Types. Holotype ♂, SURINAM. Zanderij, Boven, Para district, 25.IV.1927, Cornell University collection, genit. prep. GS-5140-SB.

Paratypes, SURINAM: 2 ♂, 2 ♀, as above but 19, 20.IV.1927 in case of ♀, Cornell 1 ♂, CNIC, Ottawa, 1 ♀; BMNH, 1 ♂, 1 ♀; genit. preps. GS-5141-SB ♀, GS-4383-SB ♀. GUYANA: 2 ♂, Tumatumari, Potaro River, 27–29.VI.1927, Cornell, genit. prep. Cornell slide no. 2 (M. Shaffer prep.).

Other material examined. GUYANA: 7 ♂, Atkinson airfield, nr. Georgetown, 1955, Lyall, BMNH (all lack abdomens); 1 ♂, Bartica, –.I.13, BMNH (no abdomen); 1 ♂, same locality, 6.V.1901, BMNH; 1 ♀, same locality BMNH, Pyral. 15355 ♀. PERU: 2 ♂, 1 ♀, Iquitos, –.V.1920, Parish, BMNH, Pyral. 15354 (1 ♂ without abdomen). BRAZIL: 1 ♀, Para (=Recife), Prov. Pernambuco, Serra de Communaty, 1.II.1893, Gounelle, BMNH; 1 ♂, 1 ♀, Amazon Reserva Ducke, km, 26, Manaus–Itacoatiara Highway, 21.IV.1971, E. G. Munro, CNIC, Ottawa.
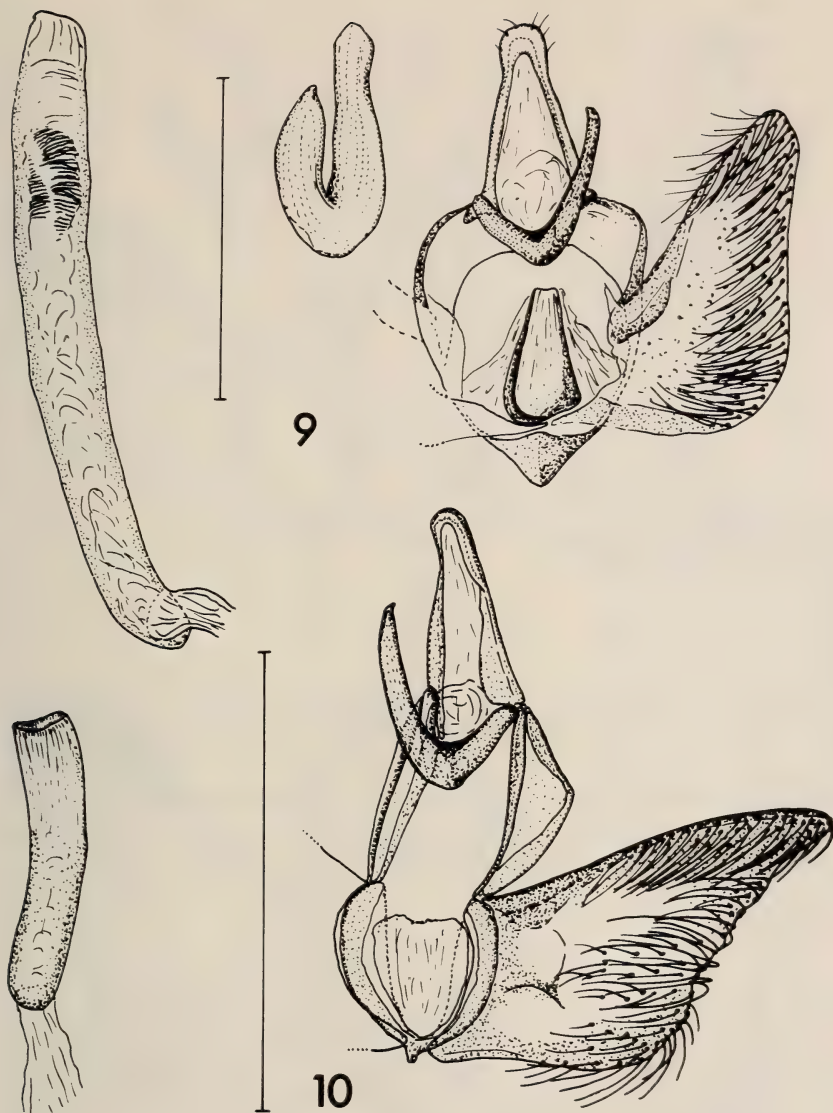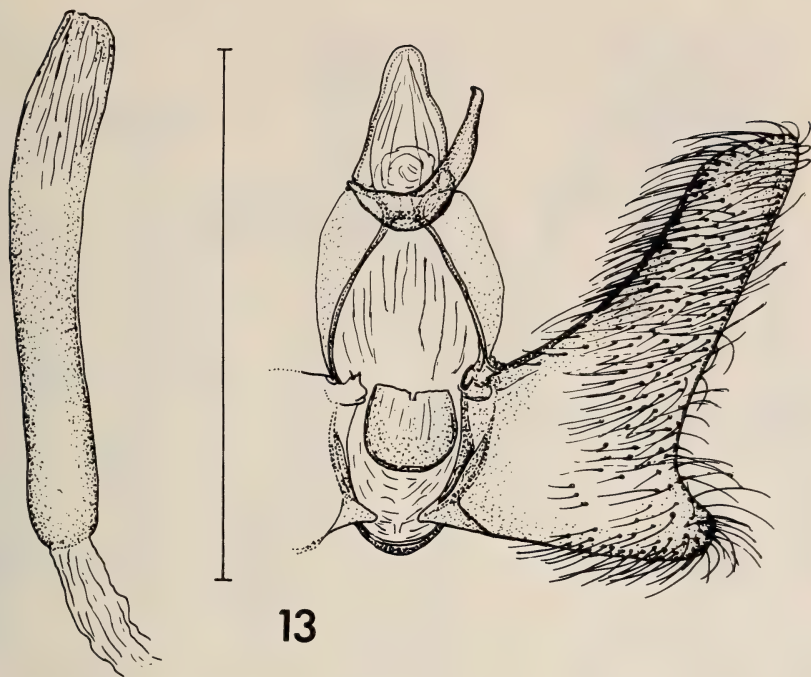
FIGS. 9, 10. Male genitalia of *Diptychophora*. **9,** *D. diasticta* holotype, aedeagus (left), transtilla in lateral aspect (center), posterior aspect of genitalia with left valva (right); **10,** *D. kuhlweini*, aedeagus (left), genitalia with left valva (right). Scale = 1 mm.

Discussion. The male and female genitalia are redescribed here. In the case of the male, Błeszynski's brief comments are ambiguous; he overlooked some structures in his drawing, and the proportions are misleading. His drawing of the female was made from a poor prepa-
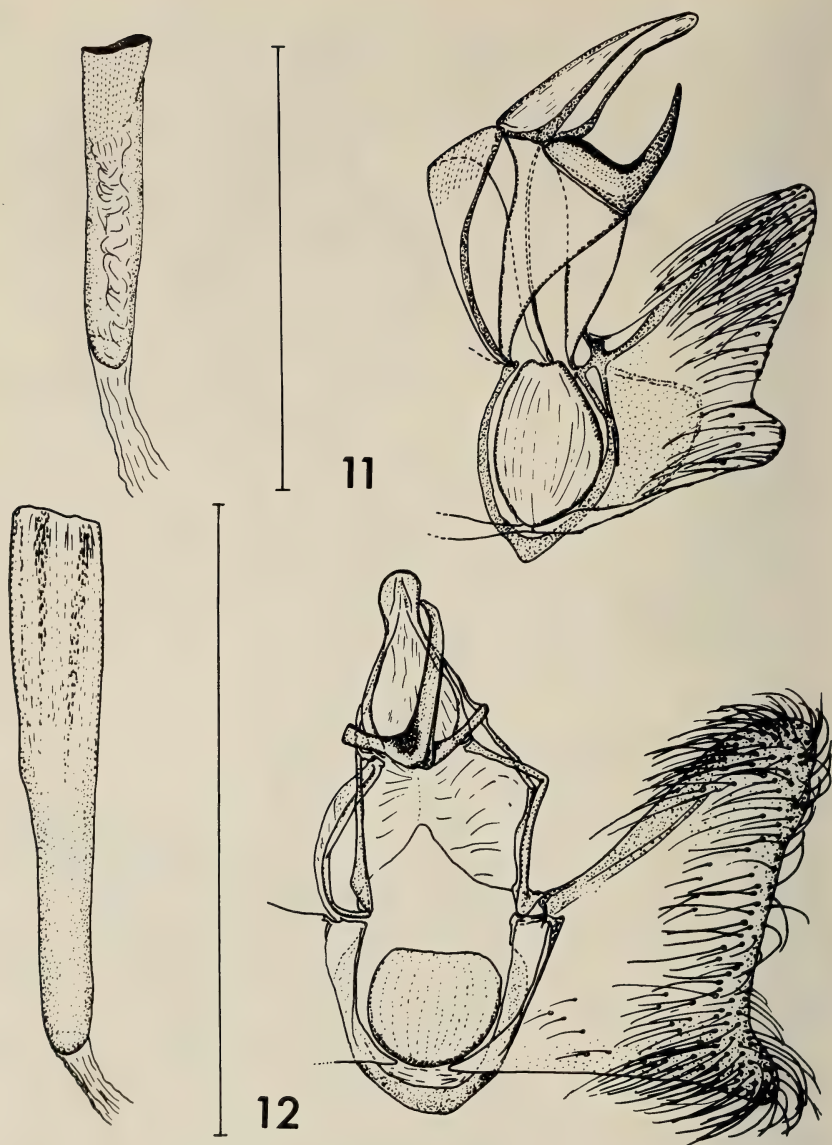
FIGS. 11, 12.   Male genitalia of *Diptychophora*. **11**, *D. subazanalis*, aedeagus (left), posterior aspect of genitalia with left valva (right); **12**, *D. desmoteria* lectotype, aedeagus (left), genitalia with left valva (right). Scale = 1 mm.

ration. The amount of material collected for this species is so great compared to some others that it must probably be either one of the commonest *Diptychophora* species, or perhaps particularly attracted to light. It has been taken in the Amazon Basin from Iquitos to Para,

FIG. 13. Male genitalia of *Diptychophora harlequinalis*, aedeagus (left), posterior aspect of genitalia with left valva (right). Scale = 1 mm.

N to the Caribbean coast and S to the edge of the Brazilian Shield; the flight period is known to include January–June. Explanation of elevation of *subazanalis* to full specific status appears in the discussion of *D. kuhlweini*.

Diptychophora incisalis (Dyar)

Colimea incisalis Dyar (1925).
*Scissolia incisalis* (Dyar); Błeszynski (1966).
Diptychophora incisalis (Dyar); Błeszynski (1967).

Exterior description (Fig. 8). Alar expanse (♀) 14–15 mm (N = 2). Details of external characteristics were adequately provided by Dyar (1925). The male is unknown.
Female genitalia (Fig. 17) (N = 1). Anal papillae weakly fused, small, about 0.5× length of posterior apophyses, 8th tergum and anterior apophyses shattered in Błeszynski's paralectotype preparation, 7th sternum tapered, rounded posteriorly. Antrum a weak funnel, ductus bursae about 6× length of posterior apophyses, ductus seminalis joining at about 0.3. Corpus bursae with single, huge strong crescentic signum, basal margin sharply turned introrse into bursae.
Types. Lectotype and paralectotype ♀, MEXICO, Colima, –.VIII.1923, Muller, type 27503, USNM, genit. prep. GS-6117-SB.

Discussion. The female genitalia are redescribed because Błeszyn-
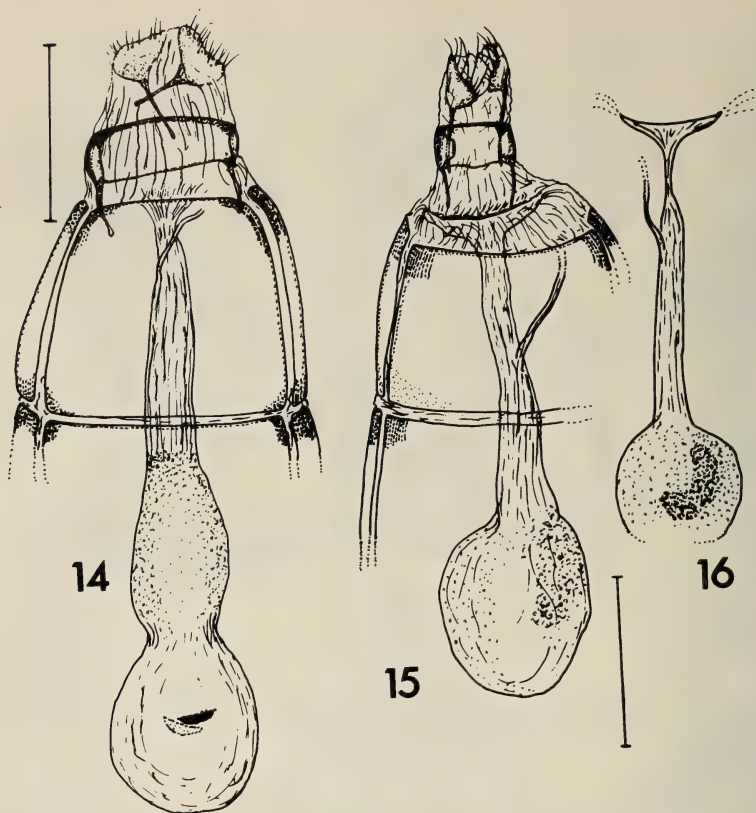
FIGS. 14–16. Female genitalia of *Diptychophora,* ventral aspect. **14,** *D. kuhlweini;* **15,** *D. subazanalis* paratype; **16,** *D. subazanalis* variation in form of signum. Scale = 1 mm.

ski's diagnosis and illustration are ambiguous. This highly patterned insect has so far been reported only from the type locality in western Mexico during August. The lectotypic series was selected by S. Bleszynski (1966).

Diptychophora desmoteria (Meyrick), new combination

Mysticomima desmoteria Meyrick (1931) (from Pyraustinae).

Exterior description (Fig. 6). Alar expanse 14–15 mm (N = 6). External characteristics were described in detail by Meyrick (1931).

Male genitalia (Fig. 12) (N = 2). Uncus simple, broad, apically rounded, spatulate, slightly constricted subapically. Gnathos triangular in cross section, curved sharply dorsad at 0.2, only slightly tapered until near the blunt apex, which is angled dorsad. Tegumen simple; juxta a suboval, relatively weak plate; saccus simple, small, rounded apically; vinculum a narrow band at valval base. Valva about 3× length of uncus, 0.8× as broad
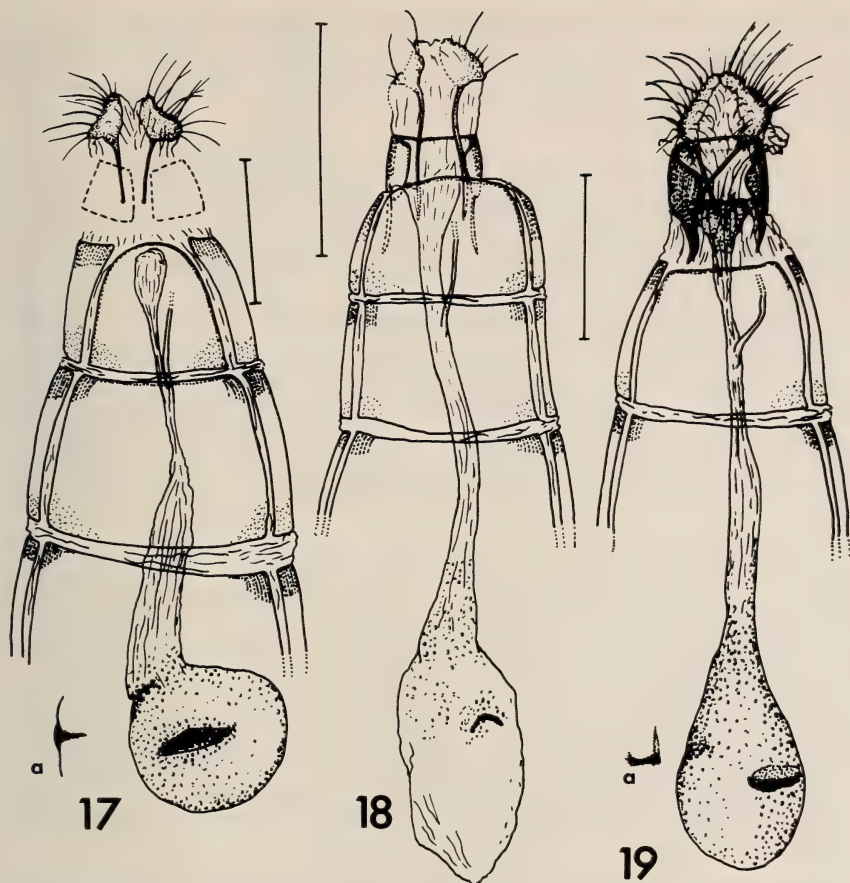
FIGS. 17–19. Female genitalia of *Diptychophora*, ventral aspect. **17,** *D. incisalis* paralectotype, **17a,** signum in lateral aspect; **18,** *D. desmoteria*; **19,** *D. harlequinalis*, **19a,** signum in lateral aspect.

as long, bifurcating into dorsal and ventral lobes, latter moderately pointed. Aedeagus about $1.2\times$ length of simple, tubular, apically expanded valva, LMB ratio about 7.5–8: 1. No cornuti.

Female genitalia (Fig. 18) ($N = 1$). Anal papillae small, weak; posterior apophyses about $3\times$ length of papillae; 8th tergum narrow, about $0.3\times$ length of posterior apophyses, anterior apophyses about $0.5\times$ posteriors; 7th sternum unmodified. Antrum a weak, simple funnel. Ductus bursae about $3.5\times$ length of posterior apophyses, ductus seminalis joining at about 0.3. Corpus bursae with single, narrow, crescentic signum.

Types. Lectotype ♂, COSTA RICA: San Jose, 1922, BMNH, genit. prep. Pyral. 15096. Selected by author and M. Shaffer (BMNH) and designated here. Paralectotypes, COSTA RICA: 3 ♂, 1 ♀, data as above, BMNH, genit. preps. Pyral. 2475 ♂, 15096 ♀.

Other material examined. 1 ♂, COSTA RICA: 3.III.24, Schmidt, BMNH.

Discussion. While curating BMNH Pyralidae, M. Shaffer noticed that *desmoteria* possessed not only a strong superficial resemblance in

both pattern and color to *Diptychophora harlequinalis,* but also the cleft forewing apex typical of most Diptychophorini. Dissection of the genitalia confirmed immediately that the species belonged in this genus, not in the Pyraustinae.

Diptychophora harlequinalis Barnes & McDunnough

Scissolia harlequinalis Barnes & McDunnough (1914).
Scissolia harlequinalis Barnes & McDunnough; Błeszynski (1966).
Diptychophora harlequinalis (Barnes & McDunnough); Błeszynski (1967).

Exterior description (Fig. 7). Alar expanse 15 mm (N = 6). External features described by Barnes and McDunnough (1914).
Male genitalia (Fig. 13) (N = 2). Uncus simple, broad, spatulate, apically rounded; gnathos triangular in cross section, tapered, curved sharply dorsad at about 0.4, apically pointed, point slightly turned dorsad. Tegumen simple, strong ventral margins; juxta a squat, semicircular, moderately sclerotized simple plate; vinculum a narrow strip at base of valva; saccus simple, small, rounded anteriorly. Valva about 3.5× length of uncus, broadly bifurcate distad, lacking costal or saccular development. Aedeagus tubular, apically truncate, slightly curved dorsad, equal to valva in length, LMB ratio 8–9:1, cornuti absent.
Female genitalia (Fig. 19) (N = 3): Anal papillae weakly fused, marginally sclerotized, posterior apophyses about 1.25× length of papillae; 8th tergum about 0.9× length of posterior apophyses; anterior apophyses present only as short, broad, pointed prongs less than length of tergum; 7th abdominal sternum unmodified. Antrum weak, flared funnel with slightly crenulate margin; ductus bursae about 6× length of posterior apophyses; ductus seminalis joining at about 0.3. Corpus bursae with single crescentic signum.
Types. Holotype ♂, U.S.A., Arizona, no date, Cornell collection.
Other material examined: USA: 1 ♂, Arizona, Oslar, Huachuca Mts., 28.VIII.1903, BMNH, genit. prep. Pyral. 15095; 1 ♀, Arizona, Madera Canyon, Santa Rita Mts., 25.VIII.1946, Comstock & Martin, Cornell, genit. prep. Cornell #2 (M. Shaffer prep.); 1 ♂, same locality, 25.VIII.1946, CNIC, Ottawa; 2 ♀, same locality, 27.VII.1947 and 3.VIII.1959, R. W. Hodges, genit. prep. EGM 1744 CNIC, Ottawa, genit. prep. EGM 1745 and 4912-SB.

Discussion. This bright yellow and black little moth has yet to be recorded outside Arizona, where its habitat is montane forest.

Steneromene, new genus

Type species ?*Zebronia azanalis* Walker (1859).

Description. Hindwing venation characterized by M_3 and Cu_1 free as in most Old World Diptychophorini, not stalked as in *Diptychophora.* Male genitalia characterized by elongate valva, definite apical lobate expansion (but not as extreme as in most species of *Diptychophora*), no development of costal region. Juxta bearing two pairs of apical horns. Saccus, vinculum exceedingly narrow. Female genitalia with eighth tergum reduced and narrow, anal papillae fused dorsally, ductus bursae bearing spinose, sclerotized subantral globate sac, ductus seminalis arising from its dorsoposterior surface, or a short distance anterior to it.

## *Steneromene azanalis* (Walker), new combination

?*Zebronia azanalis* Walker (1859).
[*Isopteryx parvalis* Walker (1865) [Erroneous synonymy by Błeszynski & Collins (1962).]
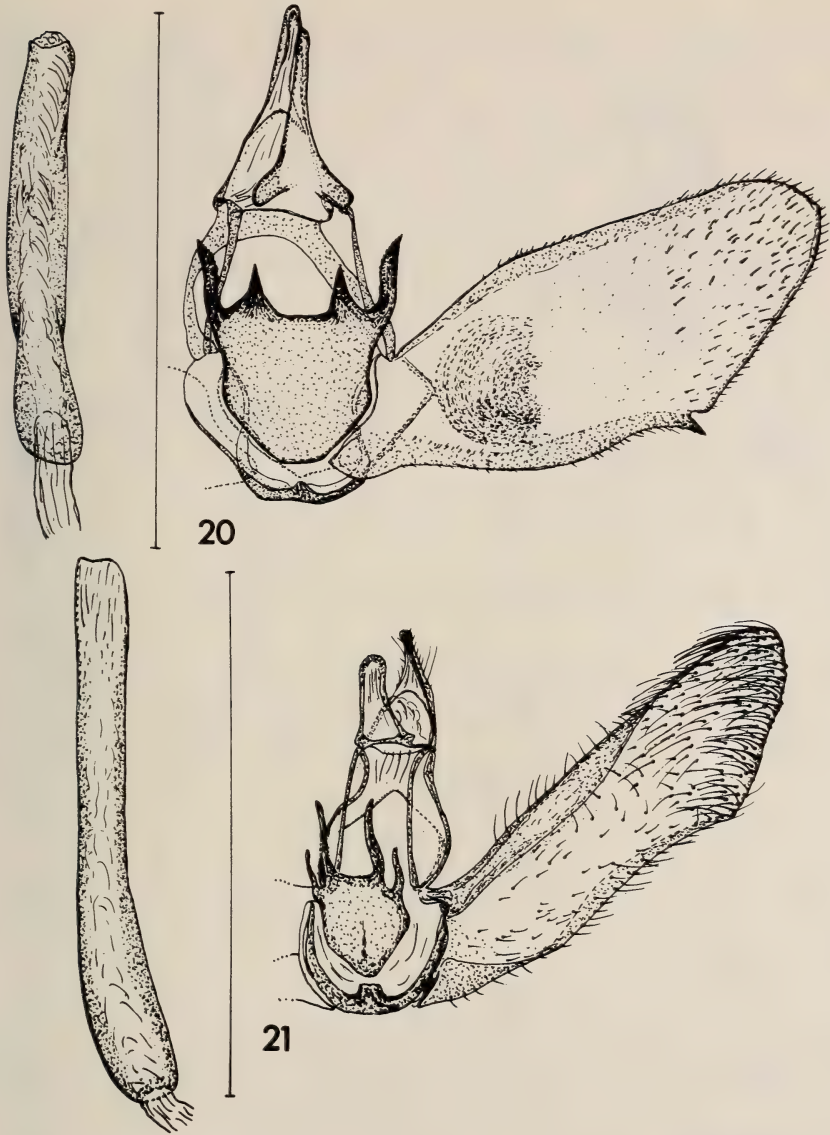
FIGS. 20, 21. Male genitalia of *Steneromene*. **20,** *S. azanalis*, aedeagus (left), posterior aspect of genitalia with left valva (right); **21,** *S. nymphocharis*, paralectotype, aedeagus (left), posterior aspect with left valva (right).

[*Diptychophora kuhlweini* Zeller (1866). [Erroneous synonymy by Błeszynski & Collins (1962).]

Diptychophora azanalis (Walker); Błeszynski & Collins (1962); Błeszynski (1967).

[*Diptychophora kuhlweini* Zeller; Błeszynski (1967). [Erroneous synonymy.]
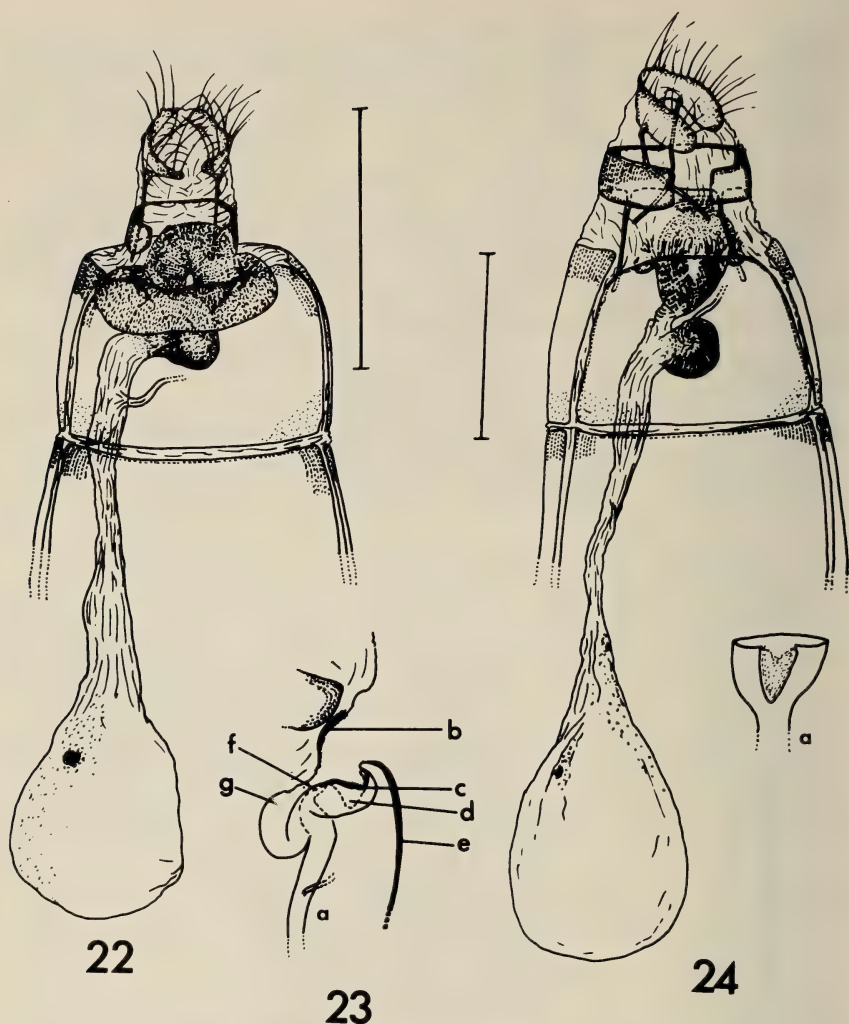
FIGS. 22–24.   Female genitalia of *Steneromene*. **22,** *S. azanalis* holotype, ventral aspect; **23,** *S. azanalis*, diagram of antrum in lateral aspect, a, ductus bursae; b, lamella postvaginalis; c, lamella antevaginalis; d, antral "pocket"; e, 7th sternum; f, antrum; g, subantral expansion; **24,** *S. nymphocharis* lectotype, ventral aspect, a, diagram of antrum, ventral aspect.

Exterior description. Alar expanse 15 mm (N = 2) (Fig. 1). Labial palpi, head, thorax, silvery white, some brown scaling. Ground color of forewings shining white, some brown scaling along costa. Basal fascia reduced to short black bar on costa near wing base. Antemedial fascia mid-brown, lateral orange shading. Postmedial fascia mid-brown, very narrow, single, virtually straight from tornus to 0.2 from costa, where it curves smoothly inwards to meet costa. Terminal zone white, except for marginal brown line with some ochre shading from 0.4–0.6, within which are two black dots. Cilia brown. Apical zone

orange ochre, with small white wedge of scales at costal extremity, and a large, irregularly shaped shining white central area, touching costa at one point, and caudally edged with black. Hindwings white, with pale brown cilia. Ventral surface pale brown, apical markings of forewing repeated from dorsal surface.

Male genitalia (Fig. 20) (N = 1). Uncus, gnathos simple, tapered, bluntly pointed. Tegumen weak except for strong posterior margins. Vinculum narrow, about 0.3 as wide as uncus is long. Saccus broad, straplike, hardly developed. Juxta strong, massive, with two pairs of apical horns, outer pair serrate on their inner margins. Valva about 2.8× length of uncus, striking concavity on inner surface from 0.2 to 0.4, costa strong but not developed into protrusions. Sacculus developed, apical prong at about 0.7 from base of valva. Aedeagus tubular, about 0.8× length of valva, cornuti absent, LMB ratio about 8:1.

Female genitalia (Figs. 22, 23a–g) (N = 1). Anal papillae broad, marginally sclerotized, about half as long as posterior apophyses. Anterior apophyses absent, 8th tergum about 0.4× length of posterior apophyses, 7th sternum not tapered posteriorly, but posterior margin in-turned to form complex lodicular structure with lamella antevaginalis, structurally a broad, heavily sclerotized ventral collar to the antrum. Lamella postvaginalis strong, suboval, fused laterally with margins of antevaginalis, forming plate dorsal to small and narrow ostium. Both lamellae spinose and scobinate. Ductus bursae with sclerotized swelling immediately below antrum proper, bulging dorsad, containing a half reverse loop of ductus bursae, the latter about 5.5–6× length of posterior apophyses, broad, weak below subantral region, ductus seminalis joining at about 0.3. Corpus bursae with single small, circular signum.

Type. Holotype ♀, BRAZIL: "Rio", "87", UMO, type slide 1193.

Other specimen examined. BRAZIL: "Rio", 1 ♂ no other data, M. Shaffer genit. prep. 1979/7 (UMO).

Discussion. I have no information on the distribution of this species; "Rio" presumably refers to Rio de Janeiro. The juxta is proportionately large and sclerotized, and there is some sclerotization of the saccular region of the male valva.

Steneromene nymphocharis (Meyrick), new combination

Diptychophora nymphocharis Meyrick (1932).
Diptychophora nymphocharis Meyrick; Błeszynski & Collins (1962).
Pareromene nymphocharis (Meyrick) Błeszynski (1967).

Exterior description (Fig. 2). External characters were described by Meyrick (1932).

Male genitalia (Fig. 21) (N = 1). Uncus simple, tapered, curved slightly ventrad, apex blunt and slightly expanded. Gnathos broad, spatulate, apically rounded with scobinate margin, membranous except for margins. Tegumen reduced, weak, prominent dorsal and ventral straplike margins. Vinculum a narrow straplike structure at base of valva. Saccus short, rounded with ventromedial strengthening. Juxta an oval plate bearing two pairs of apical horns, probably anellar in origin but firmly fused with rest of plate. Inner pair twice length of outer pair. Valva long, broad, massive in comparison to rest of genitalia, about 4.5× length of uncus; apically expanded, with beginnings of saccular fold. Costa distinct to about 0.8 on dorsal margin, without protuberances. Lateral basal coremata present. Aedeagus long, 1.1× length of valva, simple, tubular, LMB ratio about 12:1, cornuti absent.

Female genitalia (Fig. 24) (N = 1). Anal papillae strongly fused in dorsal midline; anterior apophyses about 0.7× length of posterior apophyses, 8th tergum less than half as long as anterior apophyses, 7th sternum rounded posteriorly, otherwise unmodified. Antrum a strong, scobinate, flared funnel. Lamella postvaginalis forming roof of antrum, but medially cleft. Ductus bursae about 3.5× length of posterior apophyses, ductus sem-

inalis joining at 0.3, and arising from swollen, scobinate, subantral sac. Corpus bursae bearing single, small signum.

Types. Lectotype ♀, designated here, ARGENTINA: Alta Gracia, .32, "C.B.", BMNH, genit. prep. Pyral. 15099. Paralectotypes, 1 ♂, 1 ♀, same locality but dated "2.34", BMNH, Pyral. 15100 ♂.

Discussion. Presently known only from one locality in Argentina (Sierra de Cordoba). As in *azanalis,* the male valva is not as strikingly modified from the elongate quadrate form typical of most Diptychophorini as in *Diptychophora* itself. Sclerotization of the antrum of the female ductus bursae is not as marked as in *azanalis.*

ACKNOWLEDGMENTS

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BOOK REVIEW

BUTTERFLIES OF EUROPE, vol. 1. CONCISE BIBLIOGRAPHY OF EUROPEAN BUTTERFLIES, by Otakar Kudrna. 1985. AULA-Verlag GmbH, Postfach 1366· D-6200 Wiesbaden, West Germany. 447 pp. Octavo, hard bound. $67.00 (including shipping).

This is the first in a series of planned volumes reappraising knowledge of European butterflies. Future volumes will cover all butterfly families except skippers; also, introduction to lepidopterology, ecology, and conservation. When completed, the series promises to be the most in-depth study of European butterflies, and will include taxonomy, life histories, biogeography, ecology, behavior, etc. There is a minimum of typographical errors in this first volume.

The bibliography lists about 6,000 references, primarily those between 1901 and 1983, the period before 1900 already having been covered by Horn and Schenkling, Derksen and Scheidung, Bang-Haas, Bretherton, Junk, and Kusnezov. The succinct Preface and Introduction discuss methods, purposes, history, 19th century works, and acknowledgements. Information content on ecology, biogeography, conservation, and taxonomic revision proves sparse for Europe. "The present bibliography is . . . aimed to serve the needs of all students of the butterflies of Europe, whether they take primary or secondary interest in lepidopterology, whether they are professionals or amateurs, whether they are beginning students, or experienced scientists and/or university lecturers." Kudrna estimates that over 50,000 titles bear directly or indirectly on the butterflies of Europe, with the included 6,000 being selected on merit and usefulness. He plans to update the bibliography with supplements, and eventually produce a larger, more comprehensive work of 10–15,000 references. Especially relevant to North American workers are the many general studies cited; part of our nearctic butterfly fauna was derived from the Palaearctic.

This bibliography is a useful reference source that must have been a Herculean effort to prepare. Over 80% of the references were checked against the original works for citation accuracy. Europe presents special problems because of its multitude of languages and the scattered references. The completion of the eight volumes of the *Butterflies of Europe* toward the end of this century, produced by a team of modern specialists and edited by Kudrna, promises to be a major advance in the scientific study of butterflies.

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GENERAL NOTES

OBSERVATIONS ON THE DIURNAL GREGARIOUS ROOSTING OF
OCALARIA SP. (NOCTUIDAE) IN COSTA RICA

Gregarious roosting behavior (quiescent aggregations for sleeping or passing unfavorable periods) has been documented for various diurnally active Lepidoptera (DeVries et al., Zool. J. Linn. Soc., in press). Among nocturnally active Lepidoptera, however, little evidence of a consistent roosting habit has been found. An exception is the well-documented aestivation behavior of the Australian bogong moth, *Agrotis infusa* (Boisduval) (Noctuidae). During the summer when its larval host plants are not available, adults migrate to granite outcrops and there form dense aggregations (Common 1954, Aust. J. Zool. 2:223–263) reminiscent of those formed by the North American monarch butterfly, *Danaus plexippus* (Linnaeus) (Nymphalidae). Another type of diurnal roosting in a nocturnally active species is that of the skipper butterfly, *Celaenorrhinus fritzgaertneri* (Baily) (Hesperiidae). It forms roosts in caves and hollows during the dry season in Costa Rica, apparently as a mechanism for passing a time of year when conditions for larval development are unfavorable (DeVries et al., cited above). In contrast to the bogong moth, however, *C. fritzgaertneri* adults leave and return to the roost following a synchronous circadian rhythm.

The genus *Ocalaria* (Noctuidae) was established by Schaus (1906, Proc. U.S. Nat. Mus. 30:132) for a group of moths whose phylogenetic affinities are uncertain, but which is at present tentatively placed at the end of the subfamily Ophiderinae (Erebinae of authors) in the U.S. National Museum of Natural History (NMNH) (R. W. Poole, pers. comm.). The *Ocalaria* species treated here is a small, mottled gray-brown moth with an eyespot on both upper and lower surfaces of the forewing and a wingspan of about 1.5 cm (Fig. 1). Based on NMNH collections, this undescribed species has been collected most often in tree buttresses in lowland areas of Panama (R. W. Poole, pers. comm.). We describe here a roost of the species from Costa Rica, and provide notes on its roosting behavior.

In July and August 1983, a diurnal roost of *Ocalaria* sp. was observed on six separate occasions near the Sirena Station of Parque Nacional Corcovado in southwestern Costa Rica. A group of approximately 30 individuals occupied a sheltered hollow between two moss-covered buttress roots of an unidentified canopy tree along a ridgetop trail (Fig. 2). The roost was found again in the same location the following year (July and August 1984), when a preliminary investigation of moth behavior at the roost was undertaken. No other *Ocalaria* roosts were observed in either 1983 or 1984, but in 1985 several roosts were found in the immediate area (including the original site), as well as on other ridges.

The number of moths found at the roost in 1984 varied, but on average 18–21 individuals occupied the roost during the day, as estimated by visual censuses made during 10 observation periods. The moths typically congregated during the day in the hollow portion between the buttress roots in a loosely clustered group about 1 m above ground (Fig. 3). While roosting the moths were motionless, held their wings in a partially upright position, and were well camouflaged against the textured, mossy trunk in the shady hollow (Fig. 4). Most individuals would not move unless prodded. Once when attempting to capture a specimen, we disturbed two of the moths. They flew out of the hollow and landed on the same tree about 60° around the trunk. One individual was immediately seized and eaten by an *Anolis* sp. lizard (Anolidae), predation similar to that described for the diurnally roosting skipper, *Celaenorrhinus fritzgaertneri* (Hesperiidae) (DeVries et al., cited above).

To document moth activity at the roost, and times when the roost was occupied and not occupied, two evening and two morning censuses were undertaken. A synchronous pattern similar to that observed in the cave-roosting skipper *C. fritzgaertneri* characterized both departure and return to the roost. In July and August at Parque Nacional Corcovado the sun sets at approximately 1745 h, and by 1810 h it is completely dark. On August 12, observations were begun at 1730 h. Twenty-two moths were found in the roost at that time. As nightfall approached, the moths appeared restless; some changed

FIGS. 1–4. **1,** Dorsal surface (top) and ventral surface (bottom) of a male *Ocalaria* undescribed species from Costa Rica; **2,** Buttressed tree where *Ocalaria* roost was observed; **3,** A cluster of *Ocalaria* moths in the roost; **4,** Detail of roosting *Ocalaria* individual.

position in the roost. At 1750 h two moths left their perch and began to flutter inside the hollow. A few seconds later these moths flew out of the roost. Shortly thereafter (1755 h) most of the roosting moths followed suit, first hovering from 5 to 15 seconds in the hollow before flying out into the night. By 1800 h all had left the roost. At this time the light was too dim to read handwritten notes. The departing moths, which have a weak, fluttery flight, were not observed to land on the adjacent vegetation, and these moths were never found in collections made at lights in 1984. It is not known how far from the roost they fly or what they do during the night, but they did not return to the roost until daybreak. A second observation period on August 15 showed the same pattern.

On the mornings of August 14 and 18, the moths' return to the roost was observed. Observations began at 0430 h when it was still completely dark, and no moths were found on the roost on either occasion. The first light of dawn began at about 0500 h, and thereafter light intensity increased rapidly until about 0535 h when the sun rose above the horizon; however, light levels remained low in the forest understory where the roost was located until nearly 0600 h. On August 14 the first moth to approach the roost came at 0512 h and landed almost immediately. At this time light levels were barely high enough to distinguish handwriting on a page. Three more moths entered the hollow at 0515 h, and spent 10–30 seconds hovering in the hollow before landing on the trunk. As the sky became lighter (0525 h) a large pulse of moths arrived at the roost, with several fluttering

simultaneously in the hollow for 5–20 seconds before taking positions on the trunk. By 0545 h all activity ceased, and the 18 individuals in the roost remained stationary. No more moths were seen to arrive from that time until 0615 h when the observation period ended. A similar pattern of arrival was observed on the morning of August 18.

These observations suggest that the timing of roost departure and arrival in *Ocalaria* may be closely tied to light intensity, as found in cave-roosting skippers (DeVries et al., cited above). Our observations suggest that roosting sites are important for *Ocalaria* since moths were found at the same unremarkable roost site for two consecutive years, with a fairly stable roost membership over the four-week observation period during both years. This is corroborated by further observations in Costa Rica and Panama during 1985–86, where the same roosts were found occupied by populations of *Ocalaria* over long periods. Recovery of marked individuals from the roost where they were originally captured (mark-release-recapture experiments conducted in 1985) indicates that *Ocalaria*, like the cave-roosting skippers, are "faithful" to a particular roost (Greig & DeVries, in prep.).

Although there are parallels in the roosting behavior between this species and the skipper butterfly *Celaenorrhinus fritzgaertneri*, there is little evidence that *Ocalaria* moths are roosting as an aestivation response. The roosts were first observed during the early wet season when larval resources are presumably plentiful (however, there are no host plant data available for any species in the genus), and our subsequent observations in both Costa Rica and Panama suggest that *Ocalaria* roosts may persist throughout the year.

We thank the Servicio de Parques Nacionales de Costa Rica and the personnel of Parque Nacional Corcovado for hospitality during our stay in Costa Rica. J. Rawlins identified the moth to genus and R. Poole confirmed that it is an undescribed species. I. F. B. Common and an anonymous reviewer provided helpful comments on the manuscript.

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ANNOUNCEMENT

SUPPLEMENTAL KEY WORDS FOR *JOURNAL* PAPERS

Starting with *Journal* volume 41 (1987), up to five index or key words or phrases not already in titles will appear with articles and general notes. Such words should accompany manuscripts being submitted now. Terms should be selected that, together with the title, most fully describe a paper's scope and depth. Authors are best able to select supplemental index words, but reviewers and editors can help. A comprehensive index-word resource is R. H. Foote's 188-page *Thesaurus of Entomology,* published by the Entomological Society of America in 1977.

Supplemental key words will aid the skimming reader. But more importantly, they will be used to augment and enrich the index appearing at the end of each *Journal* volume. Recent indexes have been limited to little more than species, genus, family, and author. The wealth of *Journal* content pertaining to topics such as geographic variation, host relations, phenology, predation, and reproduction, has gone largely unindexed.

Supplemental key words will make more kinds of information retrievable, and result in greater *Journal* usefulness.

WILLIAM E. MILLER, Editor

CLARIFICATION OF THE LARVAL HOST PLANT OF
EPIDEMIA MARIPOSA (LYCAENIDAE) IN NORTHERN CALIFORNIA

The larval host plant of *Epidemia mariposa* (Reakirt) has long been thought to be *Polygonum douglasii* Green (Polygonaceae) (Tietz 1972, An index to the described life histories, early stages, and hosts of the Macrolepidoptera of the continental United States and Canada, A. C. Allyn, Sarasota, Florida, 426 pp.; Pyle 1981, The Audubon Society field guide to North American butterflies, Alfred A. Knopf, New York, 916 pp.). Other *Epidemia,* especially the closely related *E. nivalis* (Boisduval), use *Polygonum douglasii* as host plants (Pyle, cited above; Howe 1975, The butterflies of North America, Double-day and Co., Garden City, New York, 633 pp.). However, other studies suggest that *Vaccinium* (Ericaceae) L. is the host plant of *E. mariposa.* In a paper describing the egg of *E. mariposa* (Coolidge 1910, Can. Entomol. 42:316), its host plant was recorded as *Vaccinium* in Yosemite. Although this record probably was for *E. mariposa,* the paper referenced by Coolidge (Lembert 1894, Can. Entomol. 26:46) recorded the butterfly that oviposited on *Vaccinium* as *Chrysophanus arota* (Boisduval) which uses *Ribes* or Goose-berry. Our recent field and laboratory studies confirm that *Vaccinium* is the larval host plant for *E. mariposa* in northern California.

On 4 August 1984 we visited Cedar Lake (1,700 m elev., 24 km southwest of Mt. Shasta), Siskiyou Co., California, to obtain females of *E. mariposa* for life history studies. No *Polygonum douglasii* was observed, yet *P. bistortoides* Pursh. was found in and around the periphery of the bog, and in neighboring marshy areas. A number of potential host plants including *P. bistortoides* were taken from the area for ovipositional studies.

Eight females of *E. mariposa* were put in oviposition chambers with varying combi-nations of plants collected from the bog, along with either *Rumex californica* Rech. or *R. crispus* L. (Polygonaceae). One female was exposed to both *Rumex crispus* and *Vac-cinium arbuscula* (Gray) Merriam. Only two eggs were oviposited, both on *V. arbuscula.* Four of the eight females were switched to *V. arbuscula,* while the remaining females were left on the *Rumex* and *Polygonum.* The following day, more than 50 eggs were oviposited by the females switched to *V. arbuscula,* while none were oviposited on the *Rumex* or *Polygonum.*

After being left at room temperature for a month, the eggs were refrigerated at 4°C. They were removed after two months, and allowed to warm to room temperature (late November 1984). Within two weeks, 10 ova hatched and the neonatal larvae were con-fined with both *Rumex crispus* and *Vaccinium corymbosum* L. (nursery stock). Larvae refused to feed on *R. crispus,* which we have found acceptable to *E. nivalis,* yet fed on fresh young shoots of *V. corymbosum.* Eggs sent to John F. Emmel were reared to maturity on *Vaccinium corymbosum.*

On 19 June 1985, we returned to Cedar Lake to look for larvae of *E. mariposa* on *Vaccinium.* By beating branches into a heavy cloth net, we obtained two mature larvae from *Vaccinium arbuscula,* but none from *V. occidentale* Gray, which also occurs in the bog. Perhaps *E. mariposa* females oviposit on particular species of *Vaccinium*; the but-terflies are not found in all areas where *Vaccinium* is abundant within their range.

A fresh female *E. mariposa* collected 27 July 1985 at Tioga Pass, Mono Co., California, was induced to oviposit on the local *Vaccinium, V. nivictum* Camp. *Vaccinium nivictum* is considered to be a close relative of *V. arbuscula* (at one time both species were considered the same as *V. caespitosum* Michx.). Unfortunately, the eggs were infertile.

Voucher specimens of *E. mariposa* from Cedar Lake are in the authors' collections and the collection of the Entomology Department, University of California at Riverside. Specimens of the *Vaccinium* are in the University's herbarium.

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POLYCHRYSIA MORIGERA (NOCTUIDAE) TRAPPED IN A SOUTHERN LADY'S-SLIPPER LABELLUM IN TENNESSEE

Catling (1974, Newsletter Mich. Entomol. Soc. 19(1):1, 3) conjectured that a skipper butterfly, *Thymelicus lineola,* might exemplify a case in which a species recently introduced into North America had not "learned" that entering labella of the showy (or queen) lady's-slipper flowers was both unproductive of nectar and likely to result in entrapment. The discovery described below extends this hypothesis to the southern lady's-slipper, *Cypripedium kentuckiense* Reed, and a plusiine noctuid moth, *Polychrysia morigera* (Edwards). The moth is a western American species which seems to have recently become established in the East.

On 24 May 1984, Medley discovered two moths inside the shoelike labellum of one flower of the southern lady's-slipper in Scott Co., Tennessee. The plant was located at the margin of a mesic floodplain forest, and was growing in a more open area than were most of the others in that population. One moth was dead, the other still alive; both were slightly worn, probably from their efforts to escape. This was the first discovery of a lepidopteran in flowers of this species during a study of lady's-slippers populations in which over 1,000 blossoms were examined in Kentucky, Tennessee, Arkansas, and Oklahoma from 1980–85. That number includes about 200 at the Scott Co. site examined at the time the moths were recovered. The only other insect found in the overall survey was a single large bee (*Xylocopa* sp.?) in a labellum in Jefferson Co., Arkansas.

Covell identified the moths as male *Polychrysia morigera,* a species previously restricted to far western states (Eichlin & Cunningham 1978, U.S. Dep. Agr. Tech. Bull. 1567, 122 pp.). However, it appeared in Kentucky in 1976 (Covell determination), and is now known from five Kentucky counties, collected from 20 May to 13 June. The only other known eastern record is a recent capture in Pennsylvania (J. G. Franclemont, pers. comm.). It is unknown from Missouri, which has been extensively surveyed for Lepidoptera (J. R. Heitzman, pers. comm.). The present record constitutes the first report of moths in southern lady's-slipper flowers, and also the first Tennessee record of *P. morigera.*

Trapping of Lepidoptera by flowers of other *Cypripedium* species has previously been reported (Arthur 1962, Proc. Entomol. Soc. Ont. 92:190–191; Stoutamire 1967, Mich. Bot. 6:159–175; Catling, cited above; Barrows 1983, J. Lepid. Soc. 37:265–267). Small bees rather than Lepidoptera appear to be pollinators of *Cypripedium* species (Stoutamire, cited above). Catling explained how no nectar is produced by the flowers, but odor and color attract bees into the lip. They then exit through small openings placed so as to force the bees to rub against pistil and anthers. These openings are too small to permit escape by butterflies. Based on a literature review, Stoutamire summarized insect relations with five *Cypripedium* species. None involved *C. kentuckiense.* The only moth record was for *Tetracis cachexiata* Guenée (Geometridae; published as *T. lorata* Grote, a synonym), reported by J. Newman to be resting on the labellum of a stemless lady's-slipper, *Cypripedium acaule* Ait., in Michigan. The only butterflies observed inside labella of any species were recorded in those of showy lady's-slipper, *C. reginae* (Walt.). These were the following skippers (Hesperiidae): *Thymelicus lineola* (Ochsenheimer), *Epargyreus clarus* (Cramer), *Polites mystic* (Edwards), and *Polites themistocles* (Latreille). Arthur (cited above) found six individuals of the European skipper, *Thymelicus lineola,* in labella of *C. reginae* in Ontario. Catling found the same skipper in "at least half" of the "about 100" flowers of showy lady's-slipper that he examined in July 1971, in Grey and Simcoe counties, Ontario. Some blossoms contained as many as five butterflies each, some alive, some dead. In early June 1972, Catling and colleagues found one flower containing a European skipper in Washtenaw Co., Michigan. Catling noted that other skipper species of similar size were more abundant in these habitats than *T. lineola,* but none found in flowers. Barrows (cited above) found up to 24 *T. lineola* in a single *C. reginae* labellum in Cheboygan Co., Michigan. He recovered 646 *T. lineola,* as well as other insects, including "geometrid moths" from an undisclosed number of blossoms examined. *Thymelicus lineola* and unidentified geometrids were also found in *C. cal-*

ceolus L., which we determined from a Barrows illustration to be the taxon now considered *Cypripedium parviflorum* Salisb. Barrow's 1978 samples consisted of 73–90% males.

Catling conjectured that because *T. lineola* had recently been introduced into North America from Europe (1910), it might not have undergone microevolution enabling it to avoid entering and becoming fatally trapped in lady's-slipper flowers. The hypothesis is plausible in light of the many trapped *T. lineola* he and Barrows reported, contrasting with a lack of common "native" skippers trapped in labella. In support of Catling's hypothesis, we suggest that *P. morigera* may also have become established in eastern North America recently, and might also be unfamiliar with the dangers of entering these flowers—a case parallel to that of the European skipper farther north.

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AVIAN PREDATION OF ALPINE BUTTERFLIES

Because direct observation of predation on butterflies is exceedingly rare (Bowers et al. 1985, Evolution 39:93–103), the following observations of avian predation on a variety of alpine butterflies may be of interest.

While studying the foraging ecology of nesting water pipits (*Anthus spinoletta* (L.)) on the Beartooth Plateau (elev. 3,300 m), Park Co., Wyoming, I observed a nesting female pipit capture and consume the following butterflies from 6–10 August 1983, all between 1721 and 1935 MDT: two *Speyeria mormonia* (Boisduval), one *Parnassius phoebus* Fabricius, and one *Euphydryas editha* (Boisduval). In each case the butterfly was flushed from the ground as the pipit foraged by walking through the tundra vegetation. The wings were torn or flicked off before the body was eaten.

That one bird was seen capturing and eating four butterflies in a relatively short time (10 h of observation) suggests that avian predation could at times cause important mortality in some alpine butterfly populations. The proposed impact of avian predation on alpine butterflies would probably not be as extreme as that documented for other, low elevation, butterflies (Calvert et al. 1979, Science 204:847–851; Fink et al. 1983, Biotropica 15:151–153; Bowers et al. 1985, Evolution 39:93–103). However, it might still be a significant factor in the demographics of narrowly distributed taxa, such as *Boloria acrocnema* Gall & Sperling (Gall 1984, Biol. Conserv. 28:111–138), especially if the breeding density of alpine birds is high where the butterflies are concentrated.

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OVIPOSITIONAL RESPONSE OF *EUREMA NICIPPE* (PIERIDAE) TO *PHYLLANTHUS TENELLUS* (EUPHORBIACEAE)

The host plants for *Eurema* spp. are mostly members of the legume subfamilies Mimosoidae and Caesalpinoidae. Most of the other members of the pierid subfamily Coliadinae feed on other plants in the legume family (Fabaceae) (Howe 1975, The butterflies of North America, Doubleday, New York). All records associated with *Eurema* larvae in the collection at the University of Florida are for various species of *Cassia* (Caesalpinoidae) (Habeck, unpubl. data). Thus I was surprised to observe adult female *Eurema nicippe* (Cramer) alight in a dense patch of the exotic Euphorbiaceae *Phyllanthus tenellus* Roxb. and display what appeared to be ovipositional behavior. During a three-hour period (0930–1230 h) on 7 October 1985 near Gainesville, Florida, I observed 46 instances of this behavior; I expected to find eggs on the *Phyllanthus* stems visited by the butterflies, and actually found 6 eggs. These were kept in petri dishes with fresh *Phyllanthus*; hatching larvae did not feed and wandered around the dishes. When offered leaves of *Cassia chamaecrista* L. (partridge-pea) three days later they immediately began feeding.

The leaves and growth form of *Phyllanthus tenellus*, a frequent weed of moist, shaded disturbed ground, strikingly resemble a usual host plant in northern Florida, *Cassia chamaecrista* (pers. observ. and Kimball 1965, The Lepidoptera of Florida, Division of Plant Industry, Florida). *Cassia chamaecrista* has pinately compound leaves, while the small leaves of *Phyllanthus tenellus* are closely arranged in a single plane along elongate side branchlets. This suggests that *E. nicippe* locates its host plant first by sight, but that because oviposition is infrequent on this incorrect host plant, secondary chemotactic responses are involved.

Another common host of *Eurema* spp. (including *E. nicippe*) in Florida is *Aeschynomene americana* L. (joint vetch), also a legume, but a distant relative of *Cassia*. Few of the other legume species are used by *Eurema* spp. The morphology of *A. americana* also strongly resembles that of *Cassia chamaecrista*. I propose that *Aeschynomene* has become a regular host plant of *Eurema* because of continued ovipositional mistakes on this common plant, and the taxonomic relatedness of *Aeschynomene* and *Cassia*. Could *Phyllanthus* eventually become a host plant for *Eurema nicippe*? If taxonomic relatedness is necessary for host switching to occur, probably not. But if biochemical similarity or an altered detoxifying system are possible, then host switching across wider taxonomic barriers might occur. If not, an improved host recognition in *Eurema* butterflies should evolve.

Within the genus *Cassia* there is a great variety of leaf morphologies. This diversity in leaf morphology could have evolved in response to the several genera and many species of *Cassia*-feeding pierids that rely on visual clues for host finding.

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The object of the Lepidopterists' Society, which was formed in May, 1947 and formally constituted in December, 1950, is "to promote the science of lepidopterology in all its branches, ... to issue a periodical and other publications on Lepidoptera, to facilitate the exchange of specimens and ideas by both the professional worker and the amateur in the field; to secure cooperation in all measures" directed towards these aims.

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Cover illustration: First stage larva of *Natada nasoni* (Grote) (Limacodidae), from Dyar 1899, J. New York Entomol. Soc. 7:61–67. Suggested by Marc E. Epstein.

Journal of

The Lepidopterists' Society

A SIMPLE INSTANT DIET FOR REARING
ARCTIIDAE AND OTHER MOTHS

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ABSTRACT. A bean-based semiartificial diet was developed empirically for rearing species of *Rhodogastria* and *Creatonotos* (Arctiidae), foodplants for which were unavailable or unknown. It was also used successfully for Heterocera in 27 genera of five families, and is likely suitable for rearing additional species of moths. Preparation of the diet is simple even in the field, and its components are inexpensive.

There are many practical reasons for attempting to rear insects on artificial diets, in particular to provide food independent of place or season. Numerous diet recipes have been published (Vanderzant 1974, Singh 1977, Singh & Moore 1985), most of which are based on either wheatgerm, wheatgerm + casein or beans. Their diversity arises mainly from their various sources of vitamins, proteins, carbohydrates, fatty acids, and preservatives. Most published diets for Lepidoptera have been tested with only one or a few closely related species, and rearing success can seldom be standardized to permit fully objective comparisons. The suitability of a certain diet for any given but untried species is thus not predictable.

Faced with the need to breed *Rhodogastria* and *Creatonotos* (Arctiidae), we considered artificial diets because the natural foodplants were either unknown or not continuously available. We also wanted a simple medium for use under field conditions in the tropics. To these ends, we modified recipes from the literature in a largely empirical fashion until we ended with an instant diet, which is cheap and easily prepared even during field work in the tropics. This simple diet also

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TABLE 1.   Recipe of semiartificial diet. For simple preparation, 6 parts of I, 1 part of agar, and 20 parts of water are combined.

Ingredients	Amount		
	%[1]	g[2]	
Bean flour[3]	15.0	75.0	
Brewer's yeast	3.5	17.5	
Ascorbic acid	0.7	3.5	
Cholesterol	0.1	0.5	
Sorbic acid	0.1	0.5	I
Methyl-p-hydroxybenzoate	0.1	0.5	
Streptomycin	0.08	0.4	
p-formaldehyde	—	0.15	
Formaldehyde (10%)	0.3		
Germ oil with α-tocopherol[4]	0.7		
Agar agar[5]	3.0	15.0	
Water	76.0	381.0	

[1] Weight/weight, except formaldehyde, which is volume/volume.
[2] To yield ca. 500 g of diet.
[3] Dried white beans ("Weiße Bohnen," *Phaseolus compressus* var. *albus*) obtained from a supermarket and pulverized by coffee grinder.
[4] 10 g α-Tocopherol + 140 ml germ oil ("Mazola® Keimöl," a salad oil produced and distributed by Maizena GmbH, Heilbronn).
[5] High gel-strength powder, research grade (SERVA, Heidelberg, New York).

appeared well suited to rearing other arctiids and a variety of species of other heteroceran families.

MATERIALS AND METHODS

Diets

Diets initially tested were based on wheatgerm, and were similar to those described by Vanderzant (1967) and Bell and Joachim (1976). These we modified by using frozen, tinned, or dried beans (*Vicia faba, Soja hispida*), testing mixtures of beans and wheatgerm in different proportions, and adding proteins, salts, and vitamins as well as leaf-powders in varying amounts. Eventually, we omitted several standard ingredients of artificial diets to create a simpler recipe. The diet we found best (Table 1) is prepared by parboiling water, and adding the agar while stirring. Other ingredients are then mixed thoroughly (preferably with an electric hand mixer) with the gelling agar. Flat plastic dishes are filled with this pap to a depth of 4 cm. Cooling and drying is allowed for up to 12 h at room temperature before storage in a refrigerator. With refrigeration, this diet can be stored for at least five weeks; in the field, smaller amounts of diet were prepared to last for three to five days.

After obtaining good rearing results with this diet, we modified it slightly to produce an instant diet which could be prepared more easily, particularly during field work in the tropics. The only departure from the original recipe is that 0.03% p-formaldehyde (solid) was sub-

stituted for formaldehyde solution; also, in the field, germ oil and α-tocopherol were omitted. Agar and a mixture of all other solid ingredients were put separately into two plastic containers, which allows for storage and transport (mailing) without refrigeration. When the diet was required, it was prepared by merely mixing agar with boiling water and adding the mixture (and oil) while stirring thoroughly. In practice, we use a 10 ml plastic container to measure 1 part of agar, 6 parts of the mixture, and 20 parts of water (or multiples thereof if more diet is required). However, these proportions work only if the beans are ground finely (as coffee for filtering), and high gel-strength agar (SERVA, Heidelberg, New York) is used; otherwise, different weight-to-volume relationships have to be determined.

Insects

Rhodogastria phaedra (Weymer) from Kenya (East Africa) and *Creatonotos transiens* (Walker) from Sumatra, Indonesia, were extensively investigated. Stocks originated from inseminated females sent to our laboratory. The foodplants of *Rhodogastria phaedra* are unknown, and the few known for other *Rhodogastria* are not available to us. *Creatonotos transiens* is a polyphagous species which we had previously reared successfully on European substitute foodplants such as *Taraxacum officinale* L.

The suitability of the simplest recipe (the instant diet) was tested with several European and tropical Lepidoptera (Table 2) to which we had unexpected access.

In routine cultures, as many as 50 neonate larvae were put into a clear plastic Petri dish (94 mm × 16 mm) containing a piece of diet (about 6 × 6 × 3 mm). Moistened filter paper was sometimes added. Later instars were kept in groups of 10 to 30 in plastic containers (200 × 200 × 95 mm), and given larger (but always 5 mm thick) pieces of diet. Every third day, larvae were transferred to a clean container with fresh diet. For quantitative rearing data, larvae were sometimes kept singly in Petri dishes.

We usually assessed the success of a diet by comparing the visual appearance of adults with field-caught specimens, and by checking the fecundity of females and the fertility of their eggs. In some cultures we also compared diets by weighing pupae, counting eggs, and measuring rates of development. For reasons given below, however, we report only on our final results, and omit the presentation of detailed data.

RESULTS

The diets of Vanderzant (1967) and Bell and Joachim (1976) were only moderately successful with *Rhodogastria* and *Creatonotos*. Better

success was achieved by using beans instead of wheatgerm, while substituting casein by albumin and/or eggs as a protein source did not have an obvious effect. Using *Phaseolus* beans as a base, we stepwise left out casein, Wesson's salt (compare Singh 1977) and/or vitamin solutions without reduced rearing success. Later, sucrose, choline chloride, and inositol were found to be unimportant additions. The resulting best recipe from our trials is given in Table 1.

With *Creatonotos* in particular, we noted a dramatic group effect: larvae kept individually resulted in pupae which were up to 30% lighter than those of larvae kept in groups of 15–20. Thus, optimal rearing does not always depend on diet composition alone; indeed, other breeding conditions can be of overriding importance.

Notable general observations were, briefly: 1. White beans (*Phaseolus compressus* var. *albus*) appeared to be a better base for artificial diet than horse-beans (*Vicia faba*); this finding supports the experience of El-Guindy et al. (1979). 2. Soaking beans (previously done by most authors, such as Shorey & Hale 1965) proved unnecessary; pulverizing the seeds greatly simplifies preparation. 3. The use of methyl-p-hydroxybenzoate and sorbic acid enables extended storage of diet without refrigeration, and combats insect pathogens. Their concentration should nevertheless be kept as low as possible, and they can be omitted if the culture is healthy, and the diet is replaced frequently. 4. The quantitative composition of diet ingredients, particularly of water, appears less important than we originally judged from the literature.

Larvae of 38 species of moths, belonging to 27 genera of five families (Table 2) accepted our simple diet and developed with no unexpected mortality to adults that did not differ noticeably in size, color, and other characteristics from field-caught material. Females invariably proved fecund and eggs fertile. Rearing success from newly hatched larvae to adults was 80–100% in all species. Most species were reared for at least four generations (*C. transiens* for 20) without exhibiting apparent changes. However, larvae of sevaral species, including *Euchromia amoena* (Möschler) (Ctenuchiidae), *Antherea pernyi* Buerin-Meneville (Saturniidae), and all Rhopalocera, refused the diet. When checking the suitability of the simple diet with the species listed above, we experienced the following: 1. Preservatives may function as antifeedants; in some species we observed refusal if the concentration of methyl-p-hydroxybenzoate was higher than 0.1%. Hirai (1976) obtained similar results, and also reported noxious effects of sorbic acid. 2. When nonbacterial pathogens affected our cultures, we cured the larvae by adding 0.15% Fumidil B (Abbot Laboratories), a pharmaceutical marketed by CEVA, Paris, to treat honeybees for *Nosema* infection. 3. Using diets can cause a delay of two to three days before

TABLE 2.   Species successfully reared on the simple diet.

Species	Origin
Arctiidae	
"Amsacta" emittens Walker	Sri Lanka
Arctia caja L.	Germany
Ammobiota festiva Hufnagel	Turkey**
Callimorpha principalis Coll.	China**
Creatonotos gangis (L.)	Sumatra, India
Creatonotos transiens (Walker)	Sumatra, Java
Cycnia mendica Cl.	Germany**
Diacrisia sannio L.	Germany
Nyctemera sp.	India*
Ocnogyna joiceyi Talbot	Morocco**
Orodemnias cervini Fallou	Germany**
Paralacydes sp.	Kenya
Pericallia ricini Fabr.	India*
Phragmatobia fuliginosa L.	Germany
Rhodogastria bubo (Walker)	Kenya
Rhodogastria carneola Hampson	Kenya
Rhodogastria luteibarba Hampson	Kenya
Rhodogastria phaedra (Weymer)	Kenya
Rhodogastria thermochroa Hampson	Kenya
Rhodogastria vitrea (Plötz)	Kenya
Rhodogastria n. spp. (4)	Kenya
Spilosoma sp.	Borneo
Spilosoma menthastri Esp.	Germany
Teracotona rhodophaea Walker	Kenya
Utetheisa pulchella L.	India*
Ctenuchiidae	
Pseudonacia sp.	Kenya
Sphingidae	
Manduca sexta L.	America
Noctuidae	
Achaea lienardi Boisd.	Kenya
Autographa gamma L.	Germany
Paradiarsia glareosa Esp.	Germany**
Polymixis serpentina Tr.	Yugoslavia**
Staurophora celsia L.	Germany**
Lymantriidae	
Euproctis lunata Hb.	India*
Olene (*Dasychira*) *mendosa* Hb.	India*
Pralis securis Hb.	India*

* M. Eckrich, pers. comm.
** K. Heuberger, pers. comm.

newly hatched larvae begin feeding. 4. Diet is best accepted by neonate larvae, and it is often difficult or impossible to switch from foodplant to diet. 5. Addition of leaf powder to the diet (such as *Taraxacum officinale* for *A. gamma*) caused some neonate larvae to start feeding earlier than on diet lacking plant material, but always increased the

mortality of the larvae, and greatly prolonged development. 6. Color might be a cue in food detection and acceptance. Larvae of *Autographa* in a choice experiment preferred diet colored green by chromoxide (compare McGinnis & Kasting 1964). However, this did not result in better rearing success.

DISCUSSION

We succeeded in our primary objective of rearing certain tropical moths whose foodplants are unknown or unavailable, and we found a diet suited to a wide spectrum of species. The diet we report not only enabled us to discover the features of previously unknown larvae, so as to facilitate search for their natural foodplants, but also to obtain adults for breeding and experimental studies.

Existing reports of rearing arctiids on artificial diets include those of Göttel and Philogene (1978) for *Pyrrharctia isabella* (J. E. Smith), Vail et al. (1967) for *Estigmene acrea* (Drury), Singh (1977) for *Hyphantria* sp., Conner et al. (1981) for *Utetheisa ornatrix*, Bathon (1977) for *Spilosoma maculata* Stoll., and Moreau (1965) for *Arctia caja* L. Most of these diets are wheat-based. In contrast, our experience with Arctiidae showed that bean-based diets yield superior results. Apparently, beans have higher nutritive value for lepidopterous larvae than wheatgerm. Bean-based diets may also be easier to prepare, and are less expensive. Salts, vitamins, certain proteins, and other ingredients used by other authors can be omitted from bean-based diets, reducing costs significantly (1 kg of our instant diet costs ca. 7 Deutsch-Marks). In broad comparisons among reports, it must nevertheless be understood that significant differences occur in the quantitave and qualitative composition of nutrients between different species/strains of beans (Schlieper 1982).

Our medium turned out to be similar to the one described for noctuids by Shorey and Hale (1965). We have not compared our results with those of others because not only do the recipes differ, but also the species and rearing conditions—variables often as important as diet composition. Furthermore, due to the lack of natural foodplants for most species, we could not compare cultures on plants with those on diets.

We cannot explain why our diet proved successful for the variety of species tested. Though our results are certainly open to further refinement, we here report our findings as they stand now, and briefly discuss our experience because our instant diet is suited to a variety of unrelated species with different foodplant requirements. Also, in contrast to many other diets, it is easy to prepare, and inexpensive, and thus may help other workers, amateur and professional. Even if it

should not prove optimal for mass rearing of a given species, our diet may facilitate culturing of species not otherwise culturable, especially in the field.

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EVOLUTION AND IDENTIFICATION OF THE NEW WORLD HAIRSTREAK BUTTERFLIES (LYCAENIDAE: EUMAEINI): ELIOT'S *TRICHONIS* SECTION AND *TRICHONIS* HEWITSON

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ABSTRACT. I revise the lycaenid genus *Trichonis* Hewitson (Theclinae: Eumaeini), establish the new combination *Trichonis hyacinthus* Cramer, and make *Papilio thenaus* Cramer 1777 a junior synonym of *P. hyacinthus* Cramer 1775. The genus consists of two species, *T. hyacinthus* and *T. immaculata,* which differ in wing pattern, forewing shape, color of androconial scales, and length of the third palpal segment. I then assess Eliot's higher classification of the Eumaeini. I examine leg, genitalia, and wing morphology, and conclude that Eliot's *Trichonis* Section is diphyletic. The unusual male foretarsus of *Trichonis* appears to have evolved independently three times in the Eumaeini.

Eliot (1973) and Clench (1964, pers. comm. 1978) proposed different higher classifications for the "New World hairstreaks" (Lycaenidae: Theclinae: Eumaeini). Eliot divided them into a *Trichonis* Section—for genera *Trichonis* Hewitson and *Micandra* Schatz—and an enormous *Eumaeus* Section—for the remaining genera (64 available names). Clench also divided these butterflies in two groups; in one he isolated *Eumaeus* Hübner (his Eumaeini), and in the other he lumped the remaining genera (his Strymonini).

The purpose of this paper is to assess the evidence for Eliot's provisional higher classification of the Eumaeini. Specifically, I consider whether the *Trichonis* Section is a monophyletic group. As basic information needed to answer this question, I revise *Trichonis. Micandra,* which Clench (1971) treated preliminarily, needed little work for the purpose of this paper. I then discuss the evidence for Eliot's classification.

Genus *Trichonis*

Trichonis consists of two species known only from males, *T. theanus* Cramer (Fig. 1a, b) and *T. immaculata* Lathy (Fig. 2a, b). In 1865, Hewitson named *Trichonis,* primarily on the basis of an unusual male foretarsus in *T. theanus,* which he described as "exarticulate, robust, and broad beyond the middle" (Fig. 7a, b). Hewitson also illustrated the "female" of *T. thenaus,* and described its foretarsus as "of the usual form, jointed and spined." Lathy (1930) pointed out that Hewitson's female was the male of a second species, which he named *T. immaculata.* Lathy did not, however, compare foreleg morphology of

FIG. 1. Adult *Trichonis hyacinthus*. (a) male upperside, (b) male underside, (c) female upperside, (d) female underside.

T. theanus and *T. immaculata*, nor did he discuss whether Hewitson's characterization of *Trichonis* was valid. No females have been associated with either species.

I propose that *Papilio hyacinthus* Cramer (Fig. 1c, d)—Cramer named all butterflies in *Papilio*—and a second phenotypically similar species (Fig. 2c, d) are the females of *T. theanus* and *T. immaculata*. Neither "female species" has been associated with males, but both share with *T. theanus* and *T. immaculata* a pastel blue or blue-green color on the frons and ventral wings that is unique among the Eumaeini. Both sexes have truncate forewings, and share similar geographical distributions. Further, genital morphology, which is discussed more fully later, indicates that both males and females belong to a similar section of the Eumaeini.

I associate female *T. hyacinthus* with male *T. theanus* and the new female with male *T. immaculata*. The bases for this action are distribution (Fig. 3) and forewing shape (Fig. 4). Briefly, *T. hyacinthus* and *T. theanus* are known only from the Guianas and Lower Amazon while the new female and *T. immaculata* occur there and in the Upper Amazon; the new female and a male of *T. immaculata* were collected
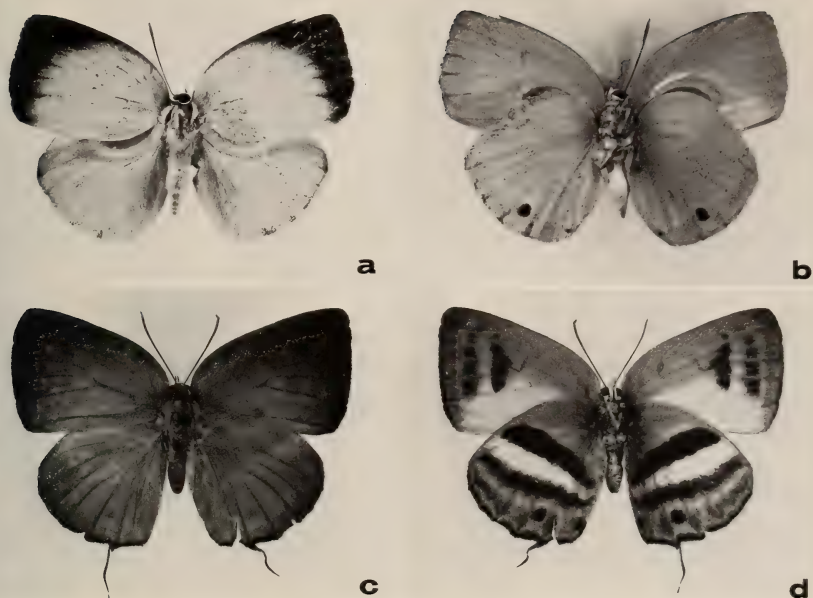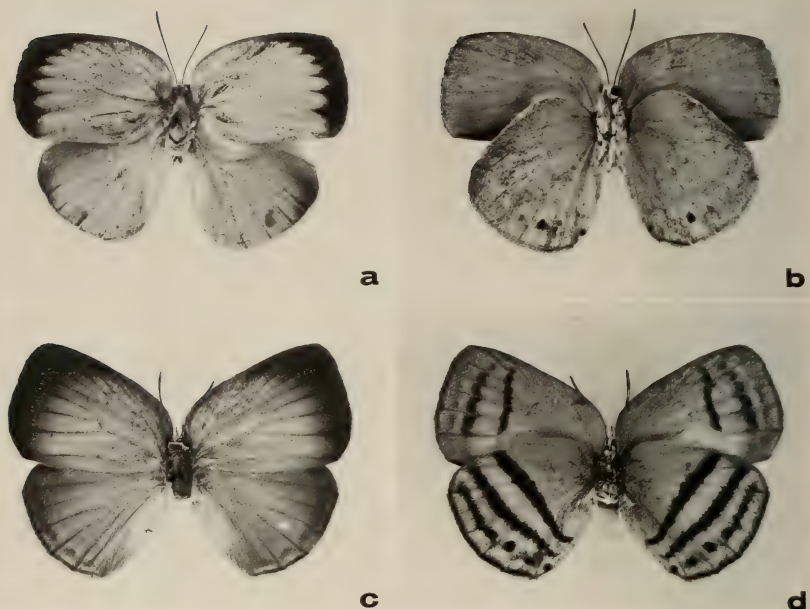
FIG. 2. Adult *Trichonis immaculata*. (a) male upperside, (b) male underside, (c) female upperside, (d) female underside.

at the same locality in northern Peru. As detailed below, the forewing apex is more truncate in male *T. immaculata* than in male *T. theanus* and in the new female than in female *T. hyacinthus*.

Characters unique to *Trichonis* include a pastel blue or blue-green frons and ventral ground color, and the genitalia, whose structure (Figs. 5 & 6) differs quantitatively from other eumaeines. I do not know which species or species group is its closest relative. *Trichonis* may be enlarged as our understanding of eumaeine phylogeny increases.

Key to *Trichonis* Species and Sexes

1. Ventral hindwings without transverse brown lines (Fig. 1b, 2b) _____ (males) . . . 2
   Ventral hindwings with transverse brown lines (Fig. 1d, 2d) _____ (females) . . . 3
2. Inner edge of dorsal forewing marginal band "smooth" (Fig. 1a), not scalloped. Ventral forewing androconial patch almost touching upper part of discal cell (Fig. 4a) _____ male *hyacinthus*
   Inner edge of dorsal forewing marginal band scalloped (Fig. 2a). Ventral forewing androconial patch barely enters discal cell (Fig. 4c) _____ male *immaculata*
3. Ventral hindwing with a white band between major brown transverse lines (Fig. 1d); hindwing with a tail _____ female *hyacinthus*
   Ventral hindwing with a blue or blue-green (ground color) band between major brown transverse lines (Fig. 2d); hindwing without a tail _____ female *immaculata*

TRICHONIS SYSTEMATICS

Nomenclature

Trichonis Hewitson (1865): Hewitson described *Trichonis* in the Lycaenidae with Cramer's *Papilio theanus* as the only species in the genus. It is the type species by monotypy (Hemming 1967). Lathy (1930) subsequently added *T. immaculata*.

Papilio hyacinthus Cramer (1775): Cramer described *Papilio hyacinthus* from the West Indies. He included a brief description and a figure of the underside, but did not mention its sex. Various authors (Fabricius 1782, Butler 1870, Draudt 1919–1920) discussed it, but their text paraphrased the original description, and illustrations were copies of Cramer's (sometimes poorly done, such as Seitz [Draudt 1919–1920]). No one has mentioned *P. hyacinthus* for more than half a century except to note that it is unknown from the West Indies (Comstock & Huntington 1943).

There is no other species with which the figure of *P. hyacinthus* can be confused; the white band sandwiched between two transverse brown lines on the ventral hindwing is distinctive. All known specimens are females.

There are no potential lectotypes in the Artis Collection, Instituut voor Taxonomische Zoölogie, Zoölogisch Museum, Universiteit van Amsterdam (Hogenes, pers. comm.), at the Rijksmuseum van Natuurlijke Historie in Leiden (de Jong, pers. comm.), or in the British Museum (Natural History) (BMNH). However, identification of Cramer's *P. hyacinthus* poses no problems, and a type is not needed. *Trichonis hyacinthus* is a **New Combination.**

Papilio theanus Cramer (1777): Cramer described *Papilio theanus* from Surinam with a brief description and a figure of the ventral surface, on which "androconial" patches are evident. Hewitson (1862–1878) illustrated the male and female, but Lathy (1930) noted that Hewitson's female is the male of a second species (which he named *Trichonis immaculata*). All known specimens are males.

Identification of *P. theanus* poses a problem. Males of both *Trichonis* species have extremely similar ventral wing patterns (Fig. 1b, 2b), and Cramer illustrated only the ventral surface. The species can be distinguished, however, by forewing shape and extent of the "polished spot" surrounding the forewing androconia. Unfortunately, the forewing shape in Cramer's illustration is inaccurate (the curvature at the forewing apex is too great for either species). The polished spot in the original illustration (in the BMNH library) extends almost to the radial vein, which is not the case in the few specimens of *T. immaculata* that I examined. However, considering the inaccuracy of other characters

FIG. 3. Distribution of *Trichonis*. Solid dots designate exact localities, hollow dots represent generalized localities such as "Surinam" or "Maranham." (a) *T. hyacinthus*, (b) *T. immaculata*.
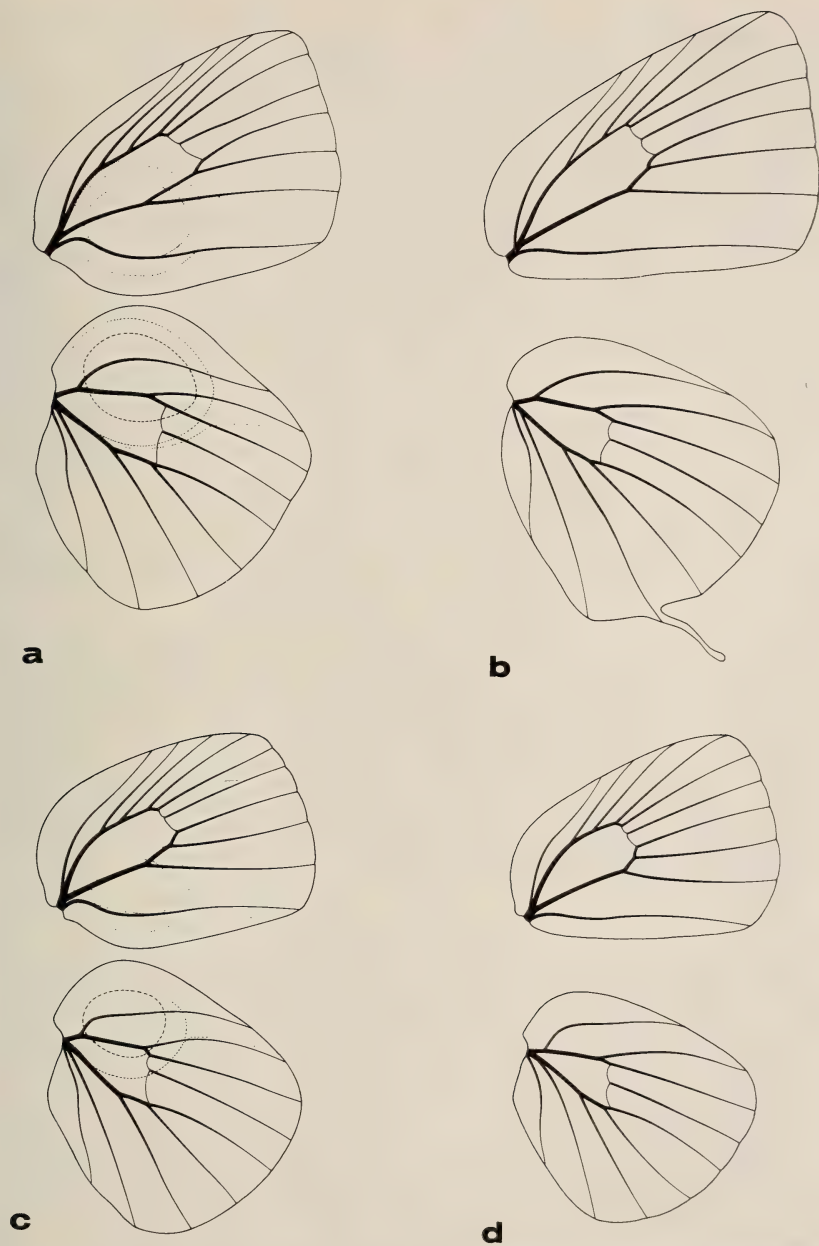
FIG. 4. *Trichonis* wing venation. (a) male *T. hyacinthus*, (b) female *T. hyacinthus*, (c) male *T. immaculata*, (d) female *T. immaculata*.

in the original figure, I hesitate to base a specific identification on so minute a detail. A type specimen is desirable.

I designate as lectotype of *P. thenaus* a specimen in the Artis Collection (Zoölogisch Museum, Amsterdam). This specimen fits Cramer's original figure well, and was probably seen by Cramer even if it was not the model for his figure. There are no potential lectotypes in Leiden or London. The specimen bears two labels: one with the number "16" and one with the text "Trichonis Theanus Cram," written in the hand of Snellen, according to Willem Hogenes, Keeper of Lepidoptera at the Zoölogisch Museum. I have added a black-bordered label which reads: "Lectotype Papilio theanus Cramer, 1777; by R. Robbins." The words "Lectotype" and "by" are printed in red and the remainder of the label is hand-written in black ink. This lectotype designation will prevent confusion in the future, and maintain the previous identifications of *P. theanus* used by Hewitson (1862–1878), Staudinger (1884–1888), Schatz and Röber (1885–1892), and Lathy (1930).

I already outlined the evidence for considering *P. theanus* to be the male of *P. hyacinthus*, and now designate *P. theanus* Cramer a junior synonym of *P. hyacinthus* Cramer; **New Synonymy.**

Trichonis immaculata Lathy (1930): Lathy described *T. immaculata* from two males: one without locality data (presumably in the Museum National D'Histoire Naturelle) and one which was the model for Hewitson's (1862–1878) "female" illustration of *T. theanus* (BMNH). Either can eventually be designated a lectotype, but identification poses no problems. Male *T. immaculata* can be distinguished from male *T. hyacinthus* (=*T. theanus*) by the "smooth" dorsal forewing border, as noted in the above key.

Geographic Distribution

Trichonis occurs in the Guianas and throughout the lowland Amazon Valley from the mouth of the Amazon River at the Atlantic Ocean to the headwaters at the base of the eastern Andes (Fig. 3). The genus is unrecorded from the West Indies except for Cramer's unverified *T. hyacinthus* record.

I examined the following specimens of *T. hyacinthus* (Fig. 3a) in the BMNH except where noted. Guyana (formerly British Guiana)— 5 males; Surinam—2 males; French Guiana (sometimes labelled Cayenne, which is thus inseparable from the present day city of that name)—5 males and 2 females, Maroni—1 female, Maroni R., St. Laurent—1 male; Brasil, Para—3 males and 1 female (1 male and 1 female in NMNH—National Museum of Natural History, Smithsonian Institution), Maranham—1 female; No Data—2 males from the Felder
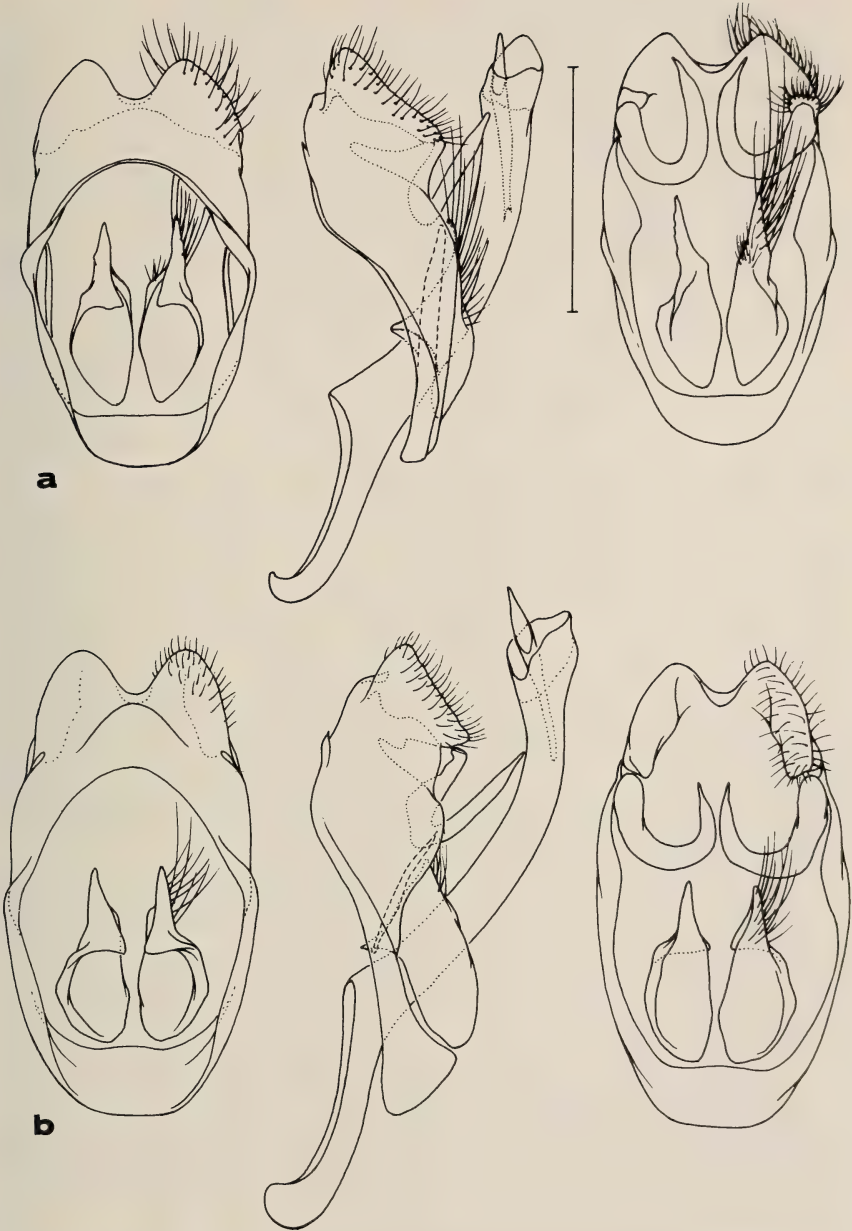
FIG. 5. *Trichonis* male genitalia. From left to right: dorsal, lateral, and ventral views. (a) *T. hyacinthus*, (b) *T. immaculata*. Scale line is 1 mm.
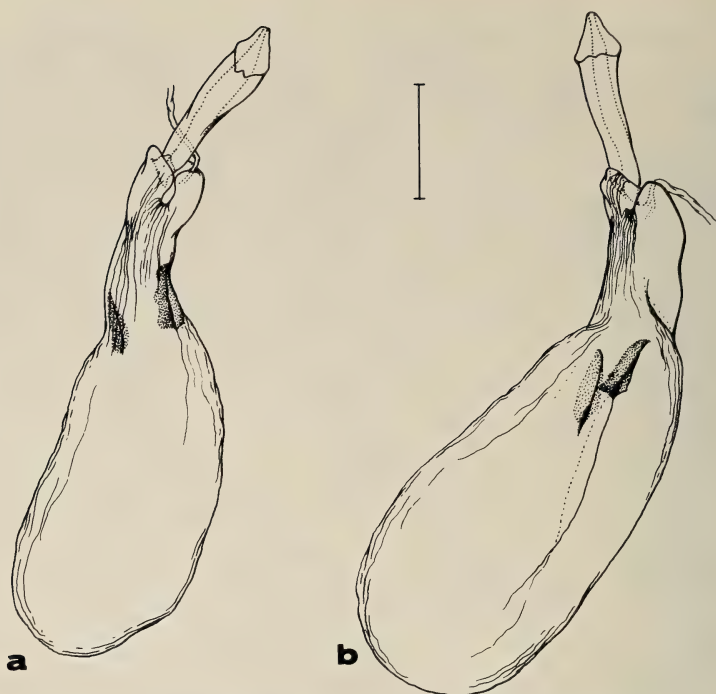
FIG. 6.   *Trichonis* female genitalia, ventral view of bursa copulatrix. (a) *T. hyacinthus*, (b) *T. immaculata*. Scale line is 1 mm.

Collection, 1 male (lectotype) in Zoölogisch Museum. None of the specimens has a date of capture.

I saw the following specimens of *T. immaculata* (Fig. 3b) in the BMNH unless otherwise noted. Surinam—1 male, Paramaribo—1 male (NMNH); French Guiana—(labelled Cayenne, Hewitson's female figure)—1 male, Gourdonville, R. Kourov—1 male; Brasil, Amazonas, Manacapuru—1 male (Carnegie Museum of Natural History); Peru—Loreto, Iquitos, Rio Cachiyaca (usually spelled Cachiyacu)—1 male and 1 female, Madre de Dios, 30 km SW of Pto. Maldonado—1 male (private collection of Dan Bogar). The Paramaribo specimen was collected in September/October, the Manacapuru specimen in May 1926, and the Madre de Dios specimen on 22 October 1983 at 0930 h.

Morphology

Antennae: 40–44 segments. The beginning of the club is not clearly defined; rather, the segments gradually increase in size and become slightly flattened (dried specimens) on either side. As a result, the club

segments are elliptically shaped. The club is composed of 18 or 19 segments. The nudum (area without scales) is found on the 5 apical segments dorsally and on the 23–24 apical segments ventrally. There are incomplete white annulations around the segments on the stalk and the first few segments of the club, where the white scaling sometimes coalesces into a short line. The few specimens with intact antennae reveal no difference between the sexes or between the species.

Eyes: The eyes have short sparse hairs, and are slightly emarginate at the antennal bases. Hewitson (1862–1868) and Draudt (1919–1920) incorrectly reported the eyes as smooth, which, if true, would have made *Trichonis* unique among the Eumaeini (Eliot 1973). There is a ring of scales (some white and some blue) surrounding the eyes, but interrupted by the antennal scape and chaetosema.

Frons: The frons is covered with downward oriented blue scales lined laterally with white scales.

Labial Palps: I measured length of the third palpal segment (with an ocular scale) because it appeared to be sexually dimorphic and to differ interspecifically. The male *T. hyacinthus* third palpal segment (mean = 0.31 mm, SD = 0.026, N = 4) is significantly shorter than the female segment (mean = 0.83, SD = 0.193, N = 3; $P < 0.05$, t-test for unequal variances, Sokal & Rohlf 1969). Likewise, this length is significantly shorter in male *T. immaculata* (male: mean = 0.40, SD = 0.011, N = 3; female: mean = 0.78, N = 1; $P < 0.01$, t-test for one observation with mean of a sample). Although such sexual dimorphism has apparently not been reported for eumaeines, a quick survey of other genera indicated that it occurs frequently. Length of the third segment is also significantly longer in male *T. immaculata* than in male *T. hyacinthus* ($P < 0.01$, t-test), contrary to Hewitson's (1862–1878) claim that they are the same. There is no evidence that the females are different ($P > 0.05$, t-test).

Thorax: Thorax, legs, and wings are covered with blue or blue-green scales. The color varies individually, not seeming to be species specific, except that the dorsal wing color of male *T. hyacinthus* is consistently more greenish than that of male *T. immaculata*.

Legs: Discussed later in the section on phylogenetic affinities.

Wing Venation: Schatz and Röber (1885–1892) figured the venation of male *T. hyacinthus* (as male *T. theanus*). The venation of both species and sexes (Fig. 4) is typical of the Eumaeini with 10 forewing veins. The position of forewing veins R_3 and M_2 varies interspecifically among eumaeine species. In *Trichonis*, forewing vein R_3 arises from the discal cell, and forewing vein M_2 arises slightly nearer vein M_1 than M_3.

Wing Shape: The forewing apex is strongly truncated in both

species—more so in males than in females and more so in *T. immac-
ulata* than in *T. hyacinthus* (Fig. 4). To show this, I measured the
angle between a line connecting the ends of veins R_1 and R_2 on the
costa and a line connecting the ends of veins M_1 and M_3 on the outer
margin. The angle of male *T. hyacinthus* was at or slightly more acute
than 90° (N = 4) while male *T. immaculata* was always more than 100°
(N = 4). Female *T. hyacinthus* ranged from 75° to 83° (N = 3). I mea-
sured the forewing angle of the single *T. immaculata* female at 87°.

Female *T. hyacinthus* is tailed at hindwing vein Cu_2 (Fig. 4b), but
neither its male nor either sex of *T. immaculata* has an indication of
a tail (Fig. 4a, c, d).

Size: I measured forewing length from the base of the radial vein to
the forewing apex as follows: male *T. hyacinthus*, mean = 1.7 cm,
SD = 0.17, N = 4; female *T. hyacinthus*, mean = 1.8 cm, SD = 0.416,
N = 3; male *T. immaculata*, mean = 1.5 cm, SD = 0.05, N = 4; female
T. immaculata, mean = 1.5 cm, N = 1.

Androconia: The venation drawings show the position and outline
of the androconial patches on the ventral forewing and dorsal hindwing
(Fig. 4). Each patch is composed of two or three parts. Forewing and
hindwing inner patches of *T. hyacinthus* are dark brown while those
of *T. immaculata* are beige. Around the inner patches, and contrasting
with them, is an area of silver scales which give the impression of being
a "polished spot." The extent of the polished area is poorly defined on
some parts of the wings, as shown by the trailing dotted lines in the
figures. The polished area immediately surrounding the inner patches
has a greenish tint, but once again, this area is poorly defined. The
extent of the polished area on the ventral forewing differs in the two
species. In *T. hyacinthus* it extends through the discal cell, and touches
or nearly touches the radial vein at the top of the cell. In *T. immac-
ulata* the polished spot extends less than half way through the cell.
(Figs. 1b, 2b do not show this difference clearly unless used in con-
junction with Fig. 4.) Eliot (1973) published an outline drawing of a
hindwing androconium in *T. hyacinthus*.

Male Genitalia (Fig. 5): Saccus almost lacking, vinculum thick ven-
trally, valvae small, penis thick with a single terminal cornutus. I found
no consistent differences between the species. The specimens illustrated
in Fig. 5 represent the extremes of individual genital variation in shape
of the valvae and ventral vinculum, and in the position of the vinculum
strut.

Female Genitalia (Fig. 6): Ductus bursae short and sclerotized, con-
cave dorsally for its entire length and twisted dextrally (not evident
from the figure). The corpus bursae is exceedingly long compared to
the ductus bursae, and is posteriorly constricted and lightly sclerotized.

The ductus seminalis, which arises from the posterior end of the corpus bursae, is "off-center" to the right side of the female. There are a pair of signa as illustrated. As with the males, there are no evident differences between the species.

Biology

Almost nothing is known about the biology of *Trichonis*. Since most of the known specimens were collected long ago, I speculate that *Trichonis* species inhabit primary forest. Because of extensive deforestation, modern visitors to the Amazon Basin rarely collect in virgin jungle. Indeed, the one recent collection of *T. immaculata* was in the Tambopata Reserve (Madre de Dios, Peru), where the jungle is protected from cutting.

Similar Species

The wing pattern of male *Trichonis* is so distinctive that it cannot be confused with that of species in other genera. Female *Trichonis*, however, are superficially similar to, and might be confused with, "*Thecla*" *tagyra* Hewitson and "*Thecla*" *floralia* Druce (which I consider a senior synonym of "*Thecla*" *tagyroides* Lathy). "*Thecla*" *tagyra* and "*T.*" *floralia* have a light blue frons and ventral ground color that is similar to *Trichonis*, but of a different quality when compared side by side. They are most easily differentiated from *Trichonis* by two superficial characters: they possess a red anal lobe on the dorsal hindwing, and black transverse lines on the ventral hindwing. *Trichonis* females lack a red anal lobe and have brown transverse lines on the ventral hindwing. I tentatively place *tagyra* and *floralia* in *Evenus* Hübner, a genus I consider unrelated to *Trichonis* on the basis of androconial structure and genital morphology.

PHYLOGENETIC AFFINITIES

Eliot (1973) placed *Trichonis* in the Eumaeini because it shares the diagnostic characters of the tribe: 10 forewing veins, "greyhound-shaped" male genitalia lacking a juxta, a stubby-tipped male foretarsus (at least in *T. immaculata*), and hairy eyes. I address the question of its phylogenetic affinities within the Eumaeini by discussing leg morphology, genitalia, and wing structures.

Legs

The lycaenid male foretarsus is unique among the Lepidoptera. The tarsomeres are fused into one segment, lack tarsal claws, are used for walking, and possess on the ventral surface "smooth-walled sensilla" with an opening at the tip and "spines"—presumed sensilla with

longitudinal striations and no opening at the tip (Fig. 8). Although male Riodinidae, Libytheidae, and Nymphalidae also have clawless foretarsi, they lack spines and smooth-walled sensilla on the foretarsus, and do not use their forelegs for walking. Some male lycaenids have a segmented and clawed foretarsus (Eliot [1973] lists genera), but evidently this structure has been independently re-expressed a number of times within the Lycaenidae (Eliot 1973, Robbins, in prep.). The male lycaenid foretarsus may be stubby-tipped (characteristic of the Eumaeini) or tapered to a sharp point (Clench 1955, Eliot 1973).

The male foretarus of *T. hyacinthus* is different from that of *T. immaculata*. The male of *T. immaculata* has a typical eumaeine foretarsus (Fig. 7c, d); it is cylindrical and stubby-tipped, and possesses spines and smooth-walled sensilla. Although Hewitson (1862–1878) claimed that it was a normal female foreleg, it lacks the claws and segmentation that occur in all lycaenid females. Unlike that of *T. immaculata*, the foretarsus of male *T. hyacinthus* (Figs. 7a, b, 8a, b), has a mid-ventral bulge (Hewitson 1862–1878), spines only at the tip (Eliot 1973), and smaller, somewhat flattened spinelike projections covering the ventral surface except for the tip. The spinelike projections, however, are striated like normal eumaeine spines (Fig. 8b), and there is a sharp transitional area of intermediate-sized spines (Fig. 8a). On the basis of this observation, I consider the spinelike projections to be small spines. Despite its unusual morphology, the male foretarsus of *T. hyacinthus* is technically lycaenid in that it is fused and possesses spines and smooth-walled sensilla (Fig. 8a).

Two other eumaeines besides *T. hyacinthus* have a stout, centrally swollen foretarsus spined only at the tip. The first is *Micandra platyptera* Felder & Felder (Figs. 7e, f, 8c, d), as Eliot (1973) noted. The foretarsus, however, lacks most of the mid-ventral bulge, and the transition in spine size is more gradual than in *T. hyacinthus*. The second species is "*Thecla*" *myrtusa* Hewitson (Figs. 7i, j, 8e, f). Its foretarsus is shaped differently than the other two, has fewer long spines at the tip, and, most notably, the small spines occur primarily on the inner face of foretarsus (not evident from the figures).

Micandra, like *Trichonis*, contains only one species with an atypical male foretarsus. Clench (1971) placed *playtptera* and *tongida* Clench in *Micandra* on the basis of venation, genitalia, and wing pattern, and listed eight other potential member species. I examined the male genitalia and venation of *ion* Druce, *comae* Druce, *cyda* Godman & Salvin, *aegides* Felder & Felder, and *amplitudo* Druce (probably a synonym of *aegides*), and all belong to *Micandra* as Clench characterized it. The "invaginated pocket" that Clench described on the male genital valvae is actually a process pointing caudally. Also, all species have
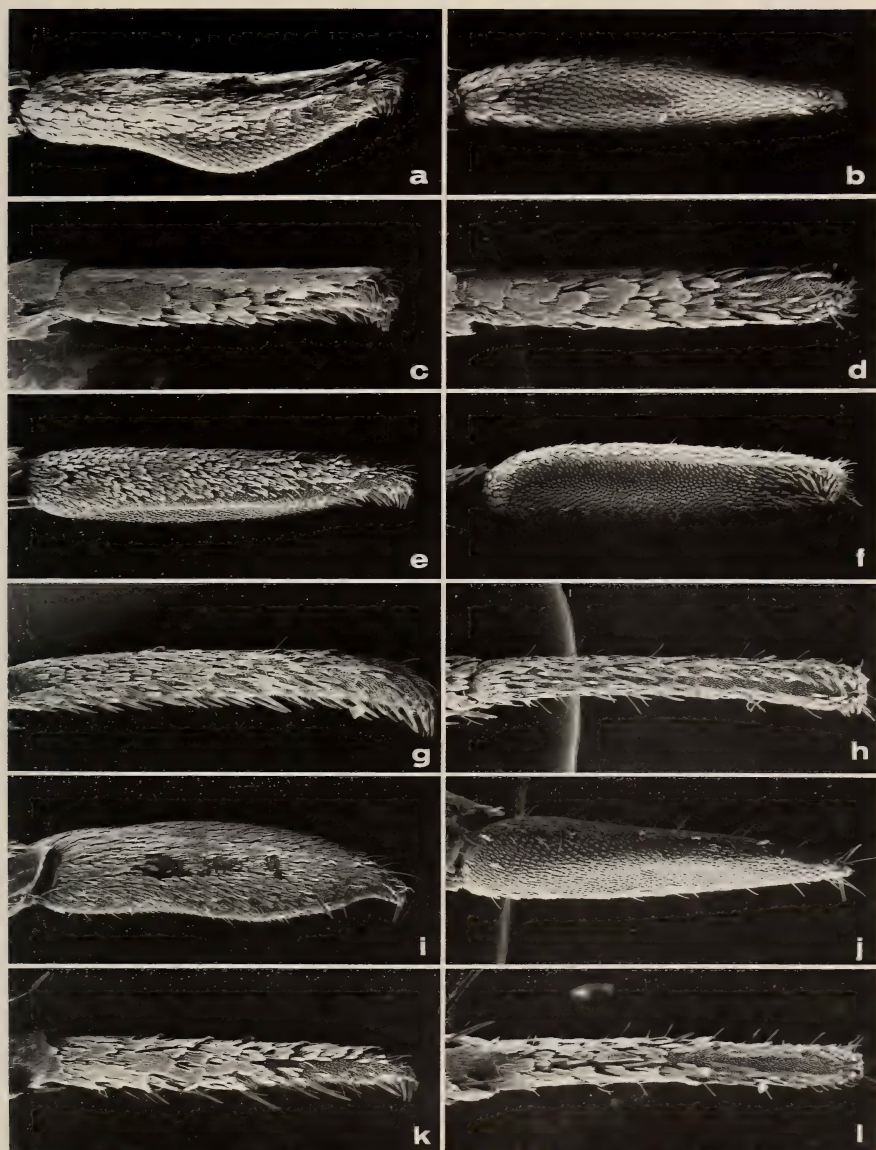
FIG. 7. Male forelegs. Lateral view on left and ventral view on right. (a & b) *T. hyacinthus*, 35×, (c & d) *T. immaculata*, 40×, (e & f) *Micandra platyptera*, 24×, (g & h) *M. comae*, 37×, (i & j) "*Thecla*" *myrtusa* — lateral view is of outer surface, two spines at tip of foretarsus are broken, 32×, (k & l) "*Thecla*" *myrtea*, 44×.

dorsal forewing androconia, contrary to Clench's key. Except for *M. platyptera*, however, these species have regularly spined male foretarsi lacking a ventral bulge (Fig. 7g, h).
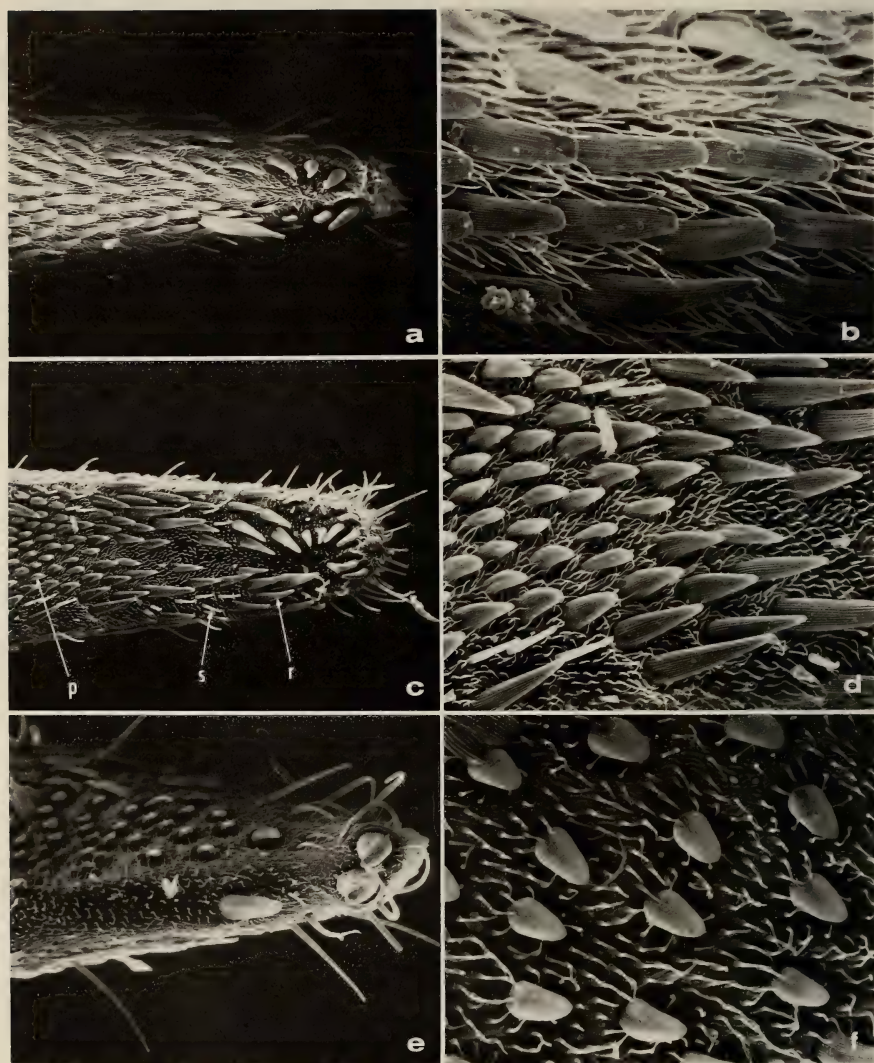
FIG. 8. Male forelegs. Ventral view. (a) *T. hyacinthus*, distal end, 110×, (b) *T. hyacinthus*, small flattened spines with striations, 525×, (c) *Micandra platyptera*, distal end, 85×, r—regular lycaenid "spine," p—small, flattened "spine," s—"smooth-walled sensillum," (d) *M. platyptera*, transition between small and regular spines, 210×, (e) *"Thecla" myrtusa*, distal end with inner face on top, 190×, (f) *"T." myrtusa*, small spines, 530×.

The species most closely related to *"Thecla" myrtusa* also lack a centrally swollen foretarsus spined only at the tip. Although phylogenetic relations are not yet worked out, *"T." myrtusa* appears to be most closely related to two groups of hairstreaks. The first group con-

tains "*Thecla*" *myrtea* Hewitson, "*T.*" *falerina* Hewitson, "*T.*" *eunus* Godman & Salvin, and "*T.*" *thara* Hewitson, and is defined by a unique dorsal hindwing "androconial" patch in which the scales have coalesced to form a thin foil-like lamination on the wing membrane. "*Thecla*" *myrtusa* shares with them a dark androconial patch at the base of the ventral forewing cubital vein, and shares a similar ventral wing pattern with "*T.*" *myrtea* and "*T.*" *falerina*. The second potential "closest relative" of "*T.*" *myrtusa* is *Allosmaitia* Clench. It shares with "*T.*" *myrtusa* beige (gray in some specimens) dorsal forewing androconia interspersed with regular wing scales, a character that Clench (1964) overlooked in *Allosmaitia*. The species in the "*T.*" *myrtea* group and in *Allosmaitia* have male foretarsi with regular rows of spines and without a central bulge (Fig. 7k, l).

"Short spines" are currently known only on the foretarsi of *T. hyacinthus, M. platyptera*, and "*T.*" *myrtusa*, but are difficult to see under a binocular microscope. Since I did not look at the male foretarsi of all their relatives under greater magnification, it is possible that some have short spines interspersed with regular ones.

Genitalia

The genitalia of *Trichonis* are quantitatively distinct from those of other eumaeines, and lack unusual qualitative characters that might be shared with other genera. Thus, in this case genital structures give, at best, an imprecise indication of relationship.

I found two major patterns of correlated genital structures among eumaeines. The first is characterized by a thick ventral vinculum, stout penis, taut manica (the membrane attaching the penis to the valvae) allowing little penial movement, no ventral processes on the lateral tegumen, and short ductus bursae with a simple cervix (the anterior ductus bursae ends abruptly with almost no change in structure). The second pattern is the antithesis of the first: a thin ventral vinculum, thin penis, loose manica, ventral processes of the tegumen present, and long ductus bursae (usually as long as the corpus bursae) with a "complex" cervix in which the shape of the anterior ductus bursae is different from the remainder of the ductus bursae. Examples of the first pattern are *Parrhasius* Hübner, *Iaspis* Kaye, *Erora* Scudder, and *Symbiopsis* Nicolay, and of the second, *Mithras* Hübner, *Evenus, Theritas* Hübner, and *Rekoa* Kaye. The two patterns represent extreme modes along a continuum of genital patterns, so that many species are intermediate and congenors may differ in one or two of these characters. However, *Trichonis* fits the first pattern while *Micandra* and "*T.*" *myrtusa* fit the second. In the absence of qualitative characters, this

evidence indicates that *Trichonis* is not phylogenetically close to *Micandra* and *"T."* *myrtusa*.

Wing Venation, Shape, Pattern, and Androconia

Trichonis wing venation is commonplace, but the truncate forewing is unusual. Although various other eumaeine species, such as *Panthiades bitias* Cramer, have truncate forewings, there are no other shared characters to support a close relation with *Trichonis*. Species in the *"Thecla"* *rocena* Hewitson complex, however, share a relatively rectangular forewing shape and ventral forewing androconia with *Trichonis*, and have broadly similar genitalia (though with many points of difference). The coxa, femur, and tibia of *"T."* *rocena* male forelegs are abnormal, but the tarsus, unlike *T. hyacinthus*, is normal. *"Thecla"* *rocena* and allies may be close relatives of *Trichonis*, but I did not find definitive evidence supporting this relation.

Wing venation may be a good indicator of *Micandra*'s relations. Both Schatz and Röber (1885–1892) and Eliot (1973) illustrated the unusual distal forewing discal cell venation, which is shared with minor variation by all species of *Micandra*. Species in other genera, such as *"Thecla"* *timaeus* Felder & Felder and relatives, also share this character, and are undoubtedly close relatives of *Micandra*.

Schatz and Röber (1885–1892) and Clench (1971) noted that *Micandra* forewing vein R_1 originates far basad of the other radials, and is situated next to Sc for most of its length. This distinctive venation is found in *Micandra*, *"Thecla"* *timaeus*, *"Thecla"* *eronos* Druce and relatives, *"Thecla"* *auda* Hewitson and relatives, and *"Thecla"* *busa* Godman & Salvin and relatives, but does not occur in either *Trichonis* or *"Thecla"* *myrtusa*. I consider it likely that this character state will eventually characterize a monophyletic assemblage of eumaeine genera, and if so, indicates that the closest relatives of *Micandra* are not *Trichonis* or *"T."* *myrtusa*.

The ventral wing pattern of *Trichonis* is unique, and does not provide clues to its systematic position. I mentioned earlier that I consider the superficial similarity between the ventral wing patterns of female *Trichonis* and two species of *Evenus* to be convergence.

Male *Trichonis* androconia on the dorsal hindwing and ventral forewing, located where the wings overlap, are also of no help in working out phylogenetic position. Many species scattered throughout the Eumaeini, as well as the Deuodorigini, a close relative of the Eumaeini (Eliot 1973), have androconia where the wings overlap. The exact structure of *Trichonis* androconial patches, as detailed above, is unique, so far as I am aware.

Eliot (1973) supported his *Trichonis* Section with the observation

that *Trichonis* and *Micandra* androconia are the same size or larger than ordinary scales—in contrast to the "small" androconia of the *Eumaeus* Section. My results do not support this observation. I found that the dorsal forewing androconia of *"Thecla" mycon* Godman & Salvin average 2.8 times larger than adjacent iridescent blue scales (N = 10). Likewise, the dorsal forewing distal androconia of *Atlides halesus* Cramer average 1.5 times larger than dorsal forewing blue scales (N = 10). Further, Eliot (1973:402) listed other species with ventral forewing androconia that are larger than "ordinary" scales. A quick survey indicated that this character state is widespread in the tribe. Further, "ordinary" wing scales can vary in size by a factor of 7 (Gray 1962). I doubt that relative androconia size will be a useful character state.

Conclusions

There are three evolutionary hypotheses that might account for the information just presented. The first hypothesis is that *T. hyacinthus*, *M. platyptera*, and *"T."* *myrtusa* form a monophyletic group defined by their male foretarsus. Consistent with this hypothesis is the observation that males of the first two species have round hindwings lacking tails while their females are tailed. However, wing pattern, genital, androconial, and venational characters are inconsistent with this hypothesis, and indicate that *T. hyacinthus* is congeneric with *T. immaculata*, *M. platyptera* with the species that Clench (1971) placed in *Micandra*, and *"T."* *myrtusa* with the *"T."* *myrtea* group and/or *Allosmaitia*. Further, sexual dimorphism in the tailed condition occurs in other eumaeines with typical eumaeine male foretarsi, such as *Erora phrosine* Druce and *"Thecla" timaeus*.

The second hypothesis is that *Trichonis*, *Micandra*, and the eventual generic assignment of *"Thecla" myrtusa* form a monophyletic group defined by the tendency to express the atypical male foretarsus. This group would approximately correspond to Eliot's (1973) *Trichonis* Section. However, there are no similarities in genitalia, venation, wing pattern, or androconia to support this hypothesis. Even the unusual tailed dimorphism mentioned in the previous paragraph occurs in only one species of *Trichonis* and one species of *Micandra*. Further, genital and venational structures, as discussed in the previous section, indicate that *Trichonis* belongs to a different group of eumaeine genera than *Micandra* and *"T."* *myrtusa*.

The third hypothesis is that the atypical male foretarsus of *T. hyacinthus*, *M. platyptera*, and *"T."* *myrtusa* has evolved independently three times. The distribution of other character states is consistent with this hypothesis, and indicates that Eliot's *Trichonis* Section is diphyletic.

An objection to this conclusion is that the repeated evolution of a qualitatively distinct foreleg is unlikely. However, the three atypical forelegs are not identical, casting doubt on their homology. Further, if a slight change during development of the male foreleg were responsible for the atypical foretarsus, then only a small genetic change, such as a mutation in a promoter or in the timing of transcription, is necessary to explain its repeated independent occurrence. Indeed, eukaryotic genes that regulate timing of development are now known (Ambros & Horvitz 1984). As the regulatory mechanisms determining development of insect leg structures are worked out, as they are being done for egg chorion structures (reviewed in Kafatos 1981) and wing pattern (Nijhout 1978, 1980a, b, 1981, 1984), it will be possible to test this idea.

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IDENTITY OF "*AUTOGRAPHA*" *OTTOLENGUII* DYAR AND OCCURRENCE OF *AUTOGRAPHA BURAETICA* (STAUDINGER) IN NORTH AMERICA (NOCTUIDAE: PLUSIINAE)

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ABSTRACT. *Autographa ottolenguii* Dyar is shown to be a typical *Syngrapha* with male genitalia similar to those of *S. nyiwonis* (Matsumura) and *S. interrogationis* (Linnaeus). The type specimen is female but has wrongly associated male genitalia. A lectotype is designated for the species. *Autographa buraetica* (Staudinger) is added to the North American noctuid fauna.

Autographa ottolenguii Dyar has been considered an anomaly because it combines *Autographa*-like male genitalia with other characters associated with *Syngrapha*.

The species was originally described as *Autographa arctica* by Ottolengui (1902) at a time when *Syngrapha* was applied only to the small, diurnal species of *Syngrapha* with yellow hind wings. Ottolengui did, however, correctly associate the species with *Autographa* [now *Syngrapha*] *interrogationis* (Linnaeus), stating that the two species differ in details of wing markings and male genitalia. Dyar (1903) renamed the species *Autographa ottolenguii* because *A. arctica* Ottolengui is a secondary homonym of the congeneric *Plusia arctica* Möschler, now considered a synonym of *Syngrapha u-aureum* (Guenée). McDunnough (1944) left the species in *Autographa* but stated that it was one of two species that he had not examined. Eichlin and Cunningham (1978) transferred the species to *Syngrapha* because of the *Syngrapha*-like female genitalia and tibial spining. They treated it as the most primitive member of *Syngrapha* because of the *Autographa*-like male genitalia. The species was returned to *Autographa* by Franclemont and Todd (1983), presumably because of the male genital characters.

I became interested in the problem while working on the Noctuidae of the Beringian area. Specimens in the Canadian National Collection (CNC) identified as *A. ottolenguii* lacked the characters typical of *Syngrapha* discussed by Eichlin and Cunningham (1978). On examination of the type specimen in the United States National Museum of Natural History, Washington, D.C. (USNM), it was immediately obvious that the CNC specimens were not conspecific. The overall appearance of the type was similar to that of the circumpolar *Syngrapha interrogationis* (Linnaeus) and to that of *S. nyiwonis* (Matsumura 1925)

FIGS. 1–4. *Syngrapha* and *Autographa* adults. 1, *Syngrapha ottolenguii* (Dyar), ♀ lectotype of *Autographa arctica* Ottolengui, Attu Island, Alaska; 2, *S. ottolenguii* (Dyar), ♂, Alaska; 3, *Autographa buraetica* (Stgr.), ♀, U.S.S.R., East Siberia, Mondy, Buryatskaya, A.S.S.R.; 4, *A. buraetica* (Stgr.), ♀, Palmer, Alaska.

of the eastern Palaearctic. The *Autographa*-like genitalia of the type (Eichlin & Cunningham 1978: fig. 68) seemed inconsistent with the otherwise typical *Syngrapha*-like appearance of the specimen, and I began to suspect that the abdomen and genital preparation were not correctly associated with the adult. Three things confirmed this suspicion: first, the male genitalia are indistinguishable from those of *Autographa californica* (Speyer); second, a second male (Fig. 2), when dissected, had genitalia typical of *Syngrapha* (Fig. 5); third, the sex of the type specimen was redetermined as female, based on the brushlike frenulum.

IDENTITY OF *SYNGRAPHA OTTOLENGUII*

The male genitalia of *Syngrapha ottolenguii* (Fig. 5) confirm the placement of the species in *Syngrapha*. Within the North American fauna, they are most like those of *S. interrogationis*, but can be distinguished by the characters in Table 1. *Syngrapha ottolenguii* is most

TABLE 1. Comparison of male genitalia of *Syngrapha* spp.

Character	*S. ottolenguii* (2 specimens)	*S. nyiwonis* (3 specimens)	*S. interrogationis* (30 specimens)
Basal cornutus (apical in vesica when everted)	straight, 1.2 mm long	straight, 1.2 mm long	absent
Apical cornutus (basal in vesica when everted)	curved, 0.6 mm long	curved, 0.6 mm long	straight, 0.4 mm long
Apex of valve	pointed	pointed	blunt
Ampulla	straight, ⅓ valve width	straight, ½ valve width	recurved, ¾ valve width
Apical third of valve	slightly expanded	narrowed	slightly expanded
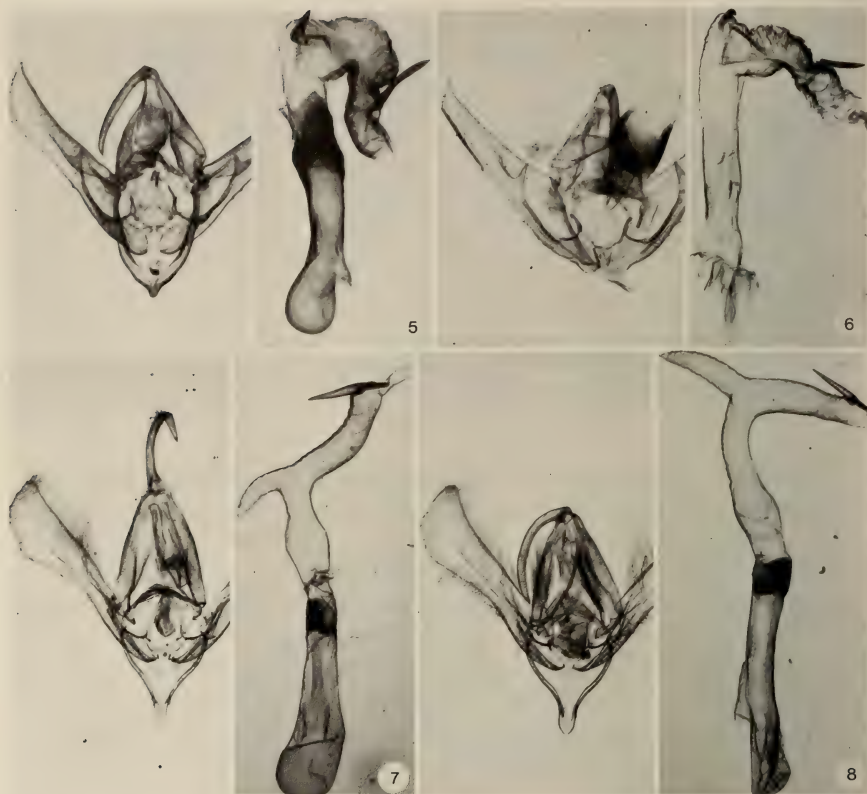
FIGS. 5–8. Male *Syngrapha* and *Autographa* genitalia with aedeagus removed and shown at right with vesica everted. 5, *Syngrapha ottolenguii* (Dyar), Alaska; 6, *S. nyiwonis* (Mats.), U.S.S.R., Magadenskaya Oblast', Kava River; 7, *Autographa buraetica* (Stgr.), Yukon, Dawson; 8, *A. pulchrina* (Haw.), England.

similar to *S. nyiwonis* (Fig. 6). The male genitalia of the two species differ only in the shape of the valve apex and in the length of the ampulla. The male genitalia of the three species are compared in Table 1.

Adults of *S. ottolenguii* can be distinguished from those of *S. interrogationis* and *S. nyiwonis* by the brownish gray rather than silvergray forewing ground color, and by the relatively straight transverse posterior line on the forewing (Figs. 1, 2).

Ottolengui described *Autographa arctica* from eight specimens in the USNM. It is not clear from the original description that one specimen was selected as holotype. Actually, one is labeled type, the others are labeled co-type. To avoid confusion, I here designate the specimen labeled type as lectotype. It is a female in good condition except that

FIGS. 9–10. Female *Autographa* genitalia. 9, *A. buraetica* (Stgr.), N.W.T., Norman Wells; 10, *A. pulchrina* (Haw.), England.

antennae and abdomen are missing. The abdomen and male genital preparation associated with the specimen are not from the lectotype. The specimen is labeled "Type No. 6258 U.S.N.M.; ♂ genit. on slide 20 Aug. 1936 JFGC 541; Genit. slide USNM 40283; *Plusia arctica* (1902) Type Ottol."

The type series was nominally collected on Alter Islands, Alaska, 8 Sept. 1880, by L. M. Turner (Ottolengui 1902). All specimens from mainland Alaska and Yukon attributed to this species have been re-identified as *Autographa buraetica* (Stgr.), discussed below. As a result, *Syngrapha ottolenguii* is known only from the type locality. After

unsuccessfully trying to locate Alter Islands, I contacted Robert Poole, who was able to provide critical information from the United States National Archives. Correspondence received by USNM in 1881 from L. M. Turner states that material collected in 1880 is from Attu, in the Aleutian Islands. Also, Turner's handwriting in this correspondence and on the specimen label makes Attu look like Alter because the first "t" is not crossed and the form of "u" resembles "er."

Syngrapha ottenlenguii is known only from Attu, and may be restricted to the outer Aleutian Islands. The species likely originated in the eastern Palaearctic 800 km to the west where its sister species *S. nyiwonis* occurs, rather than in mainland Alaska 2400 km to the east.

I believe this is the only noctuid known from the outer Aleutian Islands.

Autographa buraetica (Staudinger 1892)

Having established the identity of *Syngrapha ottolenguii*, I return to the original problem of the identity of the CNC specimens. These are *Autographa buraetica* (Staudinger), a species of the eastern Palaearctic not previously reported from North America. It can be added to a growing list of palaearctic species now known to occur in the Nearctic in Alaska and Yukon (Figs. 3, 4). *Autographa buraetica* is similar to *A. pulchrina* (Haworth) of the western Palaearctic but differs in having the thoracic tufting and forewing ground color gray-brown rather than bright reddish brown, in the length of the basal portion of the vesica (Figs. 7, 8) and in the corresponding length of the female ductus bursae (Figs. 9, 10). Thirteen North American specimens of *A. buraetica* in the CNC are from Palmer and Fairbanks, Alaska; Dry Creek, Dawson and Teslin, Yukon; Atlin in northern British Columbia; and Norman Wells in the western Northwest Territories. Collecting dates range from 27 June to 22 August. There are also two specimens from Alaska in USNM; these are from Palmer and Matamusaka.

In the North American Check List (Franclemont & Todd 1983), *Syngrapha ottolenguii* should be listed after *S. interrogationis* and *Autographa buraetica* after *A. pseudogamma* (Grote).

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THE LOCATION OF MONARCH BUTTERFLY (*DANAUS PLEXIPPUS* L.) OVERWINTERING COLONIES IN MEXICO IN RELATION TO TOPOGRAPHY AND CLIMATE

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ABSTRACT. Each year monarch butterflies migrate from breeding grounds in the United States and Canada to the Transvolcanic Belt of central Mexico. Here, within the montane fir forests, they initially aggregate in small groups of loose clusters scattered along high ridge crests. During November and December the numerous small groups consolidate into a few large compact aggregations and move downward into more protected positions closer to water. Butterfly activity increases in the last half of February due to seasonal warming. The consolidation and compaction processes that marked the beginning of the season reverse, and the colonies spread out and often split into two or more parts. After mid-March, colony size decreases as the butterflies begin to remigrate northward. Several characteristics of the climate and physiography of the Transvolcanic Belt, including moisture, altitude, and slope exposure and inclination, are important to the overwintering biology of the monarch butterfly. The forests of the zone play a major role in satisfying the overwintering monarchs' microclimatic requirements by moderating temperature extremes and conserving moisture. By colonizing this high altitude area in the tropics, the butterflies appear to satisfy microclimatic requirements that include temperatures low enough to keep activity, metabolism, and lipid expenditure to a minimum, but not so cold as to cause freezing; sufficient solar input to allow thermoregulatory basking and consequent flight; and sources of moisture and nectar.

Each autumn, millions of monarch butterflies (*Danaus plexippus* L.) migrate southwest or south (Urquhart & Urquhart 1978, Schmidt-Koenig 1979) from breeding grounds in eastern and central United States and southern Canada to overwintering sites in Mexico. Funneling through Texas, they cross into Mexico and encounter the southern extension of the Rocky Mountains, the Sierra Madre Oriental. Here they change their southwesterly course and follow the ranges to the southeast, eventually cross them, and continue to the Transvolcanic Belt, the volcanic mountains that extend across the southern end of Mexico's Central Plateau (Altiplanicie Mexicana) between 19° and 20°N latitude. At a few isolated places within the high altitude coniferous forests, which are scattered through this belt of mountains (Fig. 1), monarchs spend the winter in aggregations estimated to be in the tens of millions (Brower et al. 1977, Calvert, in prep.).

Monarchs migrate south in the fall to avoid winter cold and survive in cool, moist places where they can conserve fuel reserves in a state of reproductive inactivity until making the return trip north in the spring. Yet weather in the overwintering areas does not ideally meet monarch requirements. Not only do temperatures occasionally fall into the lethal range (Calvert et al. 1983), but also intense insolation on

clear and partly cloudy days stimulates butterfly activity to an extent that appears to contradict their need to conserve fuel. In an attempt to resolve these apparent contradictions, and to understand better why the monarchs choose these particular areas in Mexico, we here describe characteristics of the annual overwintering cycle and ecological features of several overwintering areas that we studied for nine seasons (December 1976 through spring 1985).

PHYSIOGRAPHIC FEATURES, CLIMATE AND VEGETATION

Volcanic cones and ranges dominate the terrain of the Transvolcanic Belt, which has an area of 60,000 km², and measures approximately 640 km across by 95 km wide (Moore 1945). To the north it is bounded by the high Mexican plateau, and on the south by the large Balsas River drainage (Rzedowski 1978). Its eastern portion averages 2200 m elevation with numerous peaks rising above 3600 m, including the highest mountains in North America south of Alaska (Goldman 1951). The western portion contains fewer high peaks, and declines in elevation towards the Pacific. The central area where the monarch colonies are located (Fig. 1) is drained to the north and east by the Rio Lerma and to the south and west by the Balsas-Mezcala river system (Arbingast et al. 1975).

Classic wet-dry season weather patterns prevail through most of the Transvolcanic Belt. Precipitation and heavy clouding is frequent from May until October, especially in the mountains, but winters are dry, and arid conditions prevail on the interior plains (Goldman & Moore 1945). However, winter and early spring storms occasionally occur in the area, and the higher elevations are subjected to high winds, heavy rains, snow, and ice storms (Mosina-Aleman & Garcia 1974). While potentially lethal to the overwintering butterflies (Calvert et al. 1983), these storms are also beneficial because they reduce the severity of the winter drought in the high-elevation overwintering areas.

Because of the wide range of altitudes and climatic conditions, vegetation within the Transvolcanic biotic province is extremely varied. High interior plains and valleys consist largely of grasslands intermixed with patches of small trees, shrubs, yuccas, agaves and cacti. On mountainous slopes, forests dominated by oaks and pines give way to firs at about 2750 m (Goldman 1951), but in more humid areas, the firs commence as low as 2400 m (Rzedowski 1978). On the highest peaks, firs give way to alders and other species of pine and eventually to grassland and tundra (Goldman 1951, Goldman & Moore 1945). As is true of the lower limits, vegetational transitions depend on moisture and exposure, and the altitudinal limits of the fir zone may be influ-
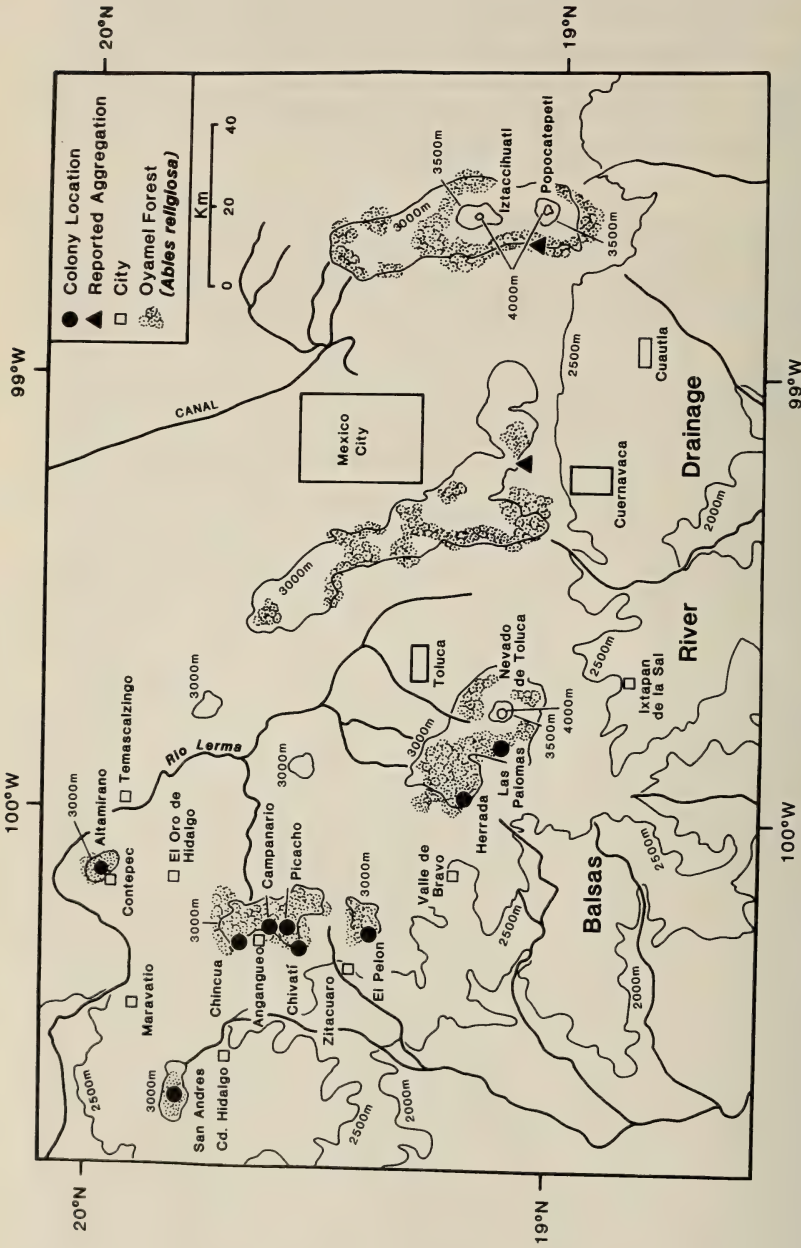
FIG. 1. Location of monarch butterfly overwintering areas in relation to topography, drainage patterns and oyamel (*Abies religiosa*) forests of Mexico's Transvolcanic Belt. Names of colonies are underlined and distribution of the oyamel forests is based on Anon. (1981). Contour interval = 500 m.

TABLE 1. Physical characteristics of 30 monarch overwintering colonies in Mexico, 1976–1982.

No.	Colony name	Date mapped	Size (ha)	Altitude (m)	Slope declination	Facing azimuth	Approximate location
						1976/77	
1	Chincua[1] 1	27 Jan	1.50	3,085	26°00'	360°	Slope of Arroyo Zapatero, Sierra Chincua, Michoacan (19°41'N, 100°18'W)
						1977/78	
2	Chincua 1	15 Jan	0.37	3,067	26°20'	4°	Slope of Arroyo Zapatero, Sierra Chincua
		2 Feb	0.76			339°	
3	Chincua 2	16 Feb	2.62	3,134	28°50'	310°	Slope of Arroyo La Plancha, Sierra Chincua
		30 Mar	0.78				Bottom of same
4	Altamirano[2]	27 Nov	0.69	3,152	26°30'	262°	Slope of Cerro Altamirano, near Contepec, Michoacan (19°58'N, 100°08'W)
		14 Feb	0.46				
5	Pelon[3]	31 Jan	1.47	3,000	18°40'	351°	Shallow canyon on Cerro Pelon, near Donato Guerra, Mexico (19°23'N, 100°16'W)
6	Herrada[4]	24 Jan	0.25	3,153	21°30'	212°	Slope of Cerro Piedra Herrada, near Valle de Bravo, Mexico (19°11'N, 99°57'W)
						1978/79	
7	Chincua 1	6 Dec	1.49	3,342	13°30'	132°	Slope of Rincon Villalobos
		11 Jan	—	3,321	20°10'	236°	Arroyo La Plancha, Sierra Chincua
8	Chincua 2	4 Nov	0.16	3,260	29°30'	193°	Slope of Arroyo La Plancha, Sierra Chincua
		12 Nov	0.53	—	—	—	
9	Chincua 3	6 Dec	0.10	3,280	29°00'	220°	Slope of Arroyo La Plancha, Sierra Chincua
10	Chincua 4	15 Nov	2.51	3,180	16°10'	230°	Slope of Arroyo Zapatero, Sierra Chincua
		13 Dec	3.29	—	—	—	
		15 Jan	2.25	3,134	—	—	
		9 Feb	2.25	—	—	—	
		3 Mar	2.72	—	—	—	Bottom of Arroyo Zapatero
		22 Mar	3.20	—	—	—	
		15 Apr	0.00	—	—	—	Colony remigrated to north

TABLE 1. Continued.

No.	Colony name	Date mapped	Size (ha)	Altitude (m)	Slope declination	Facing azimuth	Approximate location
11	Chincua 5	15 Nov	0.05	—	—	—	Upper slope of Arroyo La Plancha, Sierra Chincua
12	Chincua 6	15 Nov	0.09	—	—	—	Upper slope of Arroyo La Plancha, Sierra Chincua
13	Altamirano	14 Dec	0.19	3,200	26°30'	244°	Slope of Cerro Altamirano, near Contepec, Michoacan
						1979/80	
14	Chincua 1	9 Nov	1.20	3,290	30°00'	201°	Upper slope of Arroyo La Plancha, Sierra Chincua
		6 Jan	0.43	—	—	—	
		27 Jan	0.03	—	—	—	
15	Chincua 2	9 Nov	0.33	3,159	33°20'	219°	Upper slope of Arroyo La Plancha
		9 Jan	0.21	—	—	—	
		18 Jan	0.10	—	—	—	
16	Chincua 3	18 Jan	0.25	3,251	37°10'	218°	Upper slope of Arroyo La Plancha
17	Chincua 4	17 Jan	0.54	2,928	14°00'	239°	Bottom of Arroyo La Plancha, derived from colonies 14–16
18	San Andres	3 Dec	0.19	3,120	20°10'	207°	Slope of Cerro San Andres, near Los Asufres, Michoacan (19°47'N, 100°36'W)
						1980/81	
19	Chincua 1	22 Nov	0.92	3,155	35°40'	204°	Slope of Arroyo La Plancha, Sierra Chincua
20	Chincua 2	22 Nov	0.13	3,122	15°30'	242°	Slope of Arroyo La Plancha, Sierra Chincua
21	Chincua 3	22 Nov	0.03	3,290	25°00'	190°	Slope of Arroyo La Plancha, Sierra Chincua
22	Chincua 4	29 Nov	0.32	3,357	28°40'	179°	Slope of Arroyo La Plancha, Sierra Chincua
23	Chincua 5	30 Nov	0.12	3,171	31°40'	191°	Slope of Arroyo La Plancha, Sierra Chincua
24	Chincua 6	3 Dec	0.49	3,054	13°40'	261°	Shallow slope near bottom of Arroyo Zapatero, Sierra Chincua
		8 Jan	0.65	—	—	—	

TABLE 1. Continued.

No.	Colony name	Date mapped	Size (ha)	Altitude (m)	Slope declination	Facing azimuth	Approximate location
25		8 Feb	0.60	—	—	—	Near bottom of Arroyo La Plancha
	Chincua 7	8 Mar	—	3,019	—	—	
26	Acuña	11 Jan	2.51	3,000	31°00'	120°	Mountain SE of Cerro Los Capulines, Sierra Rancho Grande, Michoacan, local name is Acuña (19°39'N, 100°15'W)
		15 Jan	—	3,400	0°00'	—	
						1981/82	
27	Chincua	8 Feb	1.47	2,971	35°40'	150°	Slope of Arroyo La Plancha
28	Picacho 1	6 Mar	2.03	3,135	17°50'	325°	Headwaters of Arroyo La Hacienda, Sierra El Campanario, near Ocampo, Michoacan (19°35'N, 100°15'W)
29	Campanario	6 Mar	3.34	3,178	24°10'	229°	Slope of Arroyo Los Conejos, Sierra El Campanario, near Ocampo (19°00'N, 100°00'W)
30	Chivati	7 Mar	0.20	3,098	17°50'	134°	Slope of Cerro Chivatí, near Ocampo, Michoacan (19°32'N, 100°18'W)
Mean[5]			0.85	3,158	25°22'	230°18'	
SD or Angular confidence interval			0.94	118	1°	28°	

[1] The original Site Alpha area (Brower et al. 1977).
[2] The original Site Beta area (Calvert et al. 1979).
[3] The original Site Gamma area (Calvert et al. 1979).
[4] The original Site Delta area (Calvert et al. 1979).
[5] Where more than one measurement was taken, that closest to 1 February (the middle of the stable period) was chosen to compute the means and standard deviations.

enced by the presence and extent of the summer fog belt (review in Brower 1985).

HISTORY OF THE OCCURRENCE OF OVERWINTERING COLONIES

Residents of settlements located near overwintering colonies in the Sierra Chincua, Michoacan, claim that monarchs have always come to these areas. Although butterfly motifs occur widely in Precolumbian art and mythology (Brewer 1983), especially in the Teotihuacan culture (Castellanos 1983, de la Maza 1976), we have not found mention of monarch colonies in the literature prior to Urquhart's original report (1976). Lack of Precolumbian records of the conspicuous overwintering phenomenon may be due in part to its location near the boundaries of the Tarascan and Aztec empires (West 1964), which may well have been a dangerous no man's land. Possible folk-knowledge of monarchs may be expressed in the frequent use of the local Spanish name for butterfly, "paloma," in topographic features both in the overwintering areas and in areas through which they migrate. The migratory phenomenon has also found its way into the language of the Mazahua, a group of Indians living in the migratory corridor in the village of Santiago north of Villa Victoria, in the state of Mexico. Their word, "šeperito," translates as "butterfly that passes in October and November" (Kiemele Muro 1975). Historically, monarchs may have been important to the Mazahua as a supplemental food source. Collecting them at temporary roosts during the fall migration, Mazahuas still eat monarchs after removing the wings and frying them on flat ceramic pans (comals). However, the practice is now apparently limited to occasional performances for tourists (Yamaguchi 1980).

METHODS

We here depart from procedures in our previous report (Calvert et al. 1979) and name the colonies according to the mountain peak or range on which they are located. In cases where two or more colonies occupied the same peak or range in the same year, a number follows the name and signifies a specific colony location with the peak or range. Site Alpha, originally described in Brower et al. (1977), was located in the Sierra Chincua and is now called the Chincua overwintering area. Place names, geographical features and coordinates (Table 1) were determined from the Mexican CETENAL map series (Anon. 1976a).

Between December 1976 and March 1982 we spent a total of 19 months at various colonies in the Transvolcanic Belt including 94 days during 1978–79 at Chincua 4 in the state of Michoacan. During this time we located 30 colonies on 5 mountain massifs and mapped each using a Suunto sighting compass and a 100 m surveying tape. Colony

area was computed using a Hewlett-Packard double meridian distance program or an Apple II graphics program. Colony boundaries were marked with date-coded colored tape to monitor changes in positions. We recorded the declination of the mountain slope at the position of the colony and the "facing azimuth," that is, the direction of the down-slope line perpendicular to the contour at the colony center. To determine significance and angular confidence interval of the average facing azimuth, we applied circular statistics (Batschelet 1972) to azimuths, corrected for magnetic declination, approximately 8.5° east (Anon. 1976a). Circular statistics were also used to derive the angular confidence interval for the average slope declination.

During 1978–79, daily temperatures were monitored continuously from 19 January–24 March with recording hygrothermographs (Brower & Calvert 1985) at two locations, one in the forested center of Chincua 4 (Colony #10, Table 1) and the other in a nearby clearing. Forest and understory plants were identified at the University of Texas Lundell Herbarium, or by reference to Sanchez (1979).

RESULTS AND DISCUSSION

Location of Colonies

The 30 colonies we found were located in the high-altitude mountainous terrain of the Mexican Transvolcanic Belt between 19°10' and 20°00'N latitude and 99°55' and 100°40'W longitude (Table 1), a rectangle of about 7000 km² (Fig. 1). Evidence of other colonies, indicated by the presence of detached wings and body parts spread over areas up to 0.25 ha, occurred as far east as 99°52' near the volcano Nevado de Toluca. (A small colony indicated as Los Palomas in Fig. 1 was discovered here in November 1984.) Small overwintering aggregations confined to one or a few trees have been reported east of Mexico City on the western slopes of the volcanoes Popocatepetl and Ixtaccihuatl (98°45'W; J. de la Maza, pers. comm.) and south of Mexico City in the vicinity of Tres Marias (99°10'W; J. Mausan, pers. comm.). These small aggregations appear to be outlying groups that do not form every year, and no mass movement of migrant butterflies into these areas has been observed or reported.

Several locations outside the Transvolcanic Belt, and in its eastern extreme, appear to have habitat characteristics and the requisite altitude to be suitable for monarch colonies. Monarchs occasionally are seen in migration towards areas removed from known colonies. For example, in October 1980, we saw large numbers migrating SE along the escarpment above Orizaba, Veracruz, apparently headed to the Sierra de Juarez, Oaxaca. In 1977 another group was observed far from known overwintering areas and migratory pathways flying ESE near

Candelaria Loxicha, Oaxaca (de la Maza et al. 1977). Accordingly, we searched in several mountain ranges outside the known overwintering areas, including the western slopes of the Cerro Peña Nevada in the Sierra Madre Oriental, state of Nuevo Leon, in December 1977, and the western slopes of the Cofre de Perote and the Pico de Orizaba, in the states of Puebla and Veracruz in February 1980. In February 1982, our group, including Javier de la Maza of the Mexican Department of Wildlife, investigated several areas in the Sierra de Juarez and the Sierra Madre del Sur, all in the state of Oaxaca. De la Maza returned to these areas in March and early April of the same year and explored further south in the Sierra de Chiapas, eventually reaching the mountainous border of Guatemala. No colonies or evidence of colonies (such as large numbers of dismembered wings) were found.

Unless further data are forthcoming, we conclude that the principal overwintering colonies of the eastern population of the North American monarch (Fig. 1: Pelon, Chivati, Picacho, Campanario, and Chincua) occur on a few isolated mountain ranges confined to a remarkably small area of approximately 800 km² between 19°20′ and 19°45′N latitude and 100°10′ and 100°20′W longitude (at this longitude 1° of latitude = 111 km and 1° of longitude = 104 km). Scattered aggregations, such as colonies Altamirano, Herrada and San Andres (Table 1) are found outside this area, but these are always small, do not form every year, and break up earlier than those in the central area.

Colony Vegetation

Most places in the Transvolcanic Belt between 2500 and 3500 m elevation are dominated by the "oyamel" fir (*Abies religiosa* H.B.K.), which occurs on all terrain except rocky outcroppings and areas of cold air drainage (llanos). This is the major species upon which monarchs form their overwintering roosts. Other trees in the community include *Pinus pseudostrobus* Lindl. (referred to as *Pinus ayacahuite* in Brower et al. 1977), *Cupressus lindleii* Klotzsch, several species of *Quercus*, and *Buddleia cordata* H.B.K. (the last species is confined to moist canyon bottoms). *Cupressus lindleii* is found in dense stands at lower elevations within *Abies religiosa* forests, while *Pinus pseudostrobus* and *Quercus* spp. are more scattered and appear as occasional individuals within the *Abies* forest. Monarchs occasionally roost on all of these tree species but, since they mostly locate their colonies in oyamel-dominated forests, they are usually found on the oyamels. Moreover, when used as roosting trees, the broadleafed angiosperms are generally not covered as densely as are the conifers (Brower et al. 1977).

The most conspicuous components of the forest understory include tall (4 m) and medium (2 m) woody shrubs, dominated by composites,

the most important of which are *Senecio anquilifolius* D.C., *S. barba-Johannis* D.C., *Eupatorium mairetianum* D.C. and *E. patzcuarense* H.B.K. Important noncomposites in this portion of the understory are *Cestrum anagyris* Dun., *Salvia elegans* Vahl. and *S. cardinalis* H.B.K. Ground cover is dominated by *Alchemilla procumbens* Rose and one or more species of mosses in the genera *Thuidium* and *Mnium*. Local clearings contain *Senecio stoechadiformis* D.C., *S. tolucanus* D.C., *S. prenanthoides* A. Rich., *S. sanquisorbae* D.C., *Eupatorium* sp. and *Baccharis conferta* H.B.K. All of the species above, except *Alchemilla procumbens*, the *Salvia*, and the mosses, serve as monarch nectar sources at some time in the overwintering period. They also serve as substrates for drinking dew, especially in November and December.

Human disturbance is common in these forests. Lumbering without clearcutting has been practiced for many years in all overwintering areas, and many forest fires have occurred, attributable to lightning, human carelessness and, in some areas, to the practice of renewing and extending pastures. Tree densities range from over 1000/ha in young stands to about 150/ha in severely thinned forests (Calvert et al. 1982).

Colony Formation and Movement

In the Sierra Chincua, we observed colonies forming only within a narrow time range, from 2–9 November. Local foresters near the Sierra El Campanario report that butterfly arrival may vary among years by as much as two weeks and that they have arrived as early as the third week of October (P. Silva, pers. comm.). Initially, the monarchs aggregate in numerous small nuclear groups along or just below mountain ridges in dense foliage on the tops and sides of the trees. In the Sierra Chincua, dozens of these small groups form along the major NW–SE ridge above the Arroyo La Plancha and its two northwestern extensions on both sides of the Arroyo El Zapatero.

This initial phase of colony formation is characterized by much movement and intense flight activity. We hypothesize that the presence of small groups along high ridges serves as a visual cue to attract more migrants to the roosts. Apparent signalling during this early part of the overwintering season may also occur through an additional and most remarkable behavior in which the butterflies form large towering spirals. We have seen these columns of soaring butterflies in early November extending vertically at least to the limits of 10× binoculars (300 m) above ridges and clearings near colonies which were in the process of formation.

The many small nuclear groups may move about and reform at other locations or coalesce with others, and by early November they are scattered along the ridges just below the crests for distances up to 3–4

FIG. 2.   Trees coated with thick layer of rime and ice on a ridge above Chincua 6 (Colony 24, Table 1), 24 January 1981. The colony is located just outside photograph to the lower right. Exposed trees along the ridge are those on which first colony formation frequently takes place.

km. Movement continues into December and gradually the many smaller groups coalesce into a few (1–5) larger ones located further downslope, but always less than 200 m below the ridge crests. Fall migrants continue arriving during November and early December.

Consolidation into these larger groups continues through December with some colonies increasing in size at the expense of others. For example, during 1978/79, six groups were in the Chincua area on or before 6 December (Table 1). By early January, four had almost disappeared, and at least one of the two remaining ones had grown. During 1980–81, all five colonies at Chincua mapped in November had moved by 11 January from their positions on the upper slopes of Arroyo La Plancha to form a large (2.51 ha) colony lower down in the canyon (Table 1).

A major advantage of the movement of colonies from positions on high ridges to lower protected areas is the avoidance of the high altitude southwest winds and occasional storms that occur during the overwintering season (Mosino Aleman & Garcia 1973). This was dramatically illustrated in January 1981, when moisture-laden, gale-force winds covered the vegetation on an exposed ridge, where all of the groups had initially formed, with heavy ice and rime (Fig. 2). Note that the

rime and ice did not form on trees in the protected valley below the ridge where the butterflies had established their colony. But even such sheltered butterflies can be dislodged by the tens of thousands from their roosts by high winds, rain, snow, or hail (Calvert et al. 1983). Once on the ground, they are subject to increased risk of mortality from freezing (Calvert & Brower 1981, Calvert & Cohen 1983) as well as mouse predation (Brower et al. 1985).

During the first phase of colony formation in November and December, the butterflies usually occupy only the outer periphery of tree branches, and rarely settle on trunks. However, by early to mid-January, they pack onto trunks and branches of the mid-sections of trees, avoid the upper quarters of crowns, and usually also avoid the lower branches. Packing into the interior branches and onto the trunks results in decreasing the total area occupied by the colony (Fig. 3a–c). On steeper slopes and for a short while after a colony has moved and resettled, clustering may occur on the lower branches as well. Clustering on trunks occurs in two ways. During normal weather, the butterflies form trunk and bough clusters in the same manner by flying up to a group of butterflies and landing. Following storms, the many thousands of dislodged individuals crawl up from the ground onto any vertical surface until they encounter butterflies or other obstacles. In this way they form the spectacular clusters which often extend nearly the full length of the trunk (Fig. 4).

Colony Location and Movement in Relation to Moisture Requirements

Overwintering in the high mountainous forests of the Transvolcanic Belt positions the colonies in a wetter habitat than that prevailing over much of Mexico during the winter. These conditions are due to a pattern of moist subtropical air masses that move east from the Pacific in late winter and early spring. When these air masses encounter the higher mountains west of the Continental Divide, adiabatic cooling results in cloud formation and precipitation, and a more even distribution of yearly precipitation than at lower elevations (Mosino Aleman & Garcia 1974, Anon. 1973: Landsat photo).

In years with ample rainfall, consolidation and movement cease by January. The colonies are typically located in protected habitats in a shallow, moist canyon along or near the headwater of a stream, where they remain until late February or March. Some colonies persist on mountain slopes unassociated with depressions, but almost without exception a source of water is located within less than 1 km.

Notwithstanding the wetter conditions at higher elevations where the colonies are located, long spells of dry weather do occur. During

FIG. 3. Seasonal movement and size change of colony Chincua 4 from shortly after its formation in fall 1978 to its breakup in spring 1979. On 22 March a third fragment of the colony was 1 km downstream and is not shown in F. Contour interval = 20 m.

these times, tens of thousands of butterflies fly out of the colonies to drink in sunny areas along streams, moist patches or at reservoirs. Because of the distance of the colony from water, the butterflies must expend significant amounts of lipid (Chaplin & Wells 1982) in their watering flights. During exceptionally dry years, entire colonies may move downward and reform along or near water. For example, during 1979–80, when no rain occurred in the Sierra Chincua from 15 December to 9 February, three colonies located on the dry upper slopes of the Arroyo La Plancha moved about 0.5 km downslope (300 m elevation) during three weeks and reconsolidated into a single colony at the juncture of two streams (Colony 17, Table 1).

In addition to these occasional large-scale movements down to moister and more sheltered areas, colonies move incrementally or "creep" downslope during overwintering. This is explained as follows: On sunny days the thousands of butterflies that fly out of the colony return later the same day and reform their clusters on those portions of the lower colony periphery exposed to the sun. During winter afternoons, when most return, this is the southwest side. Cluster reformation occurs on the lower side of the colony because this part is usually closest to the water source. The net effect is a slow movement of the colony downslope, or down canyon, depending on where the parent colony is located. During periods of warm weather, when greater numbers travel out to water each day, this downslope creep can be rapid.

The relation of the butterflies' return route from water to the direction of colony movement was made clear in one notable exception to the above pattern. On 14 February 1978, a small, new segment of Colony 4 (Table 1) was located upslope 25 m northeast of the previously mapped colony. Instead of returning to the colony directly from the water source located to the south at the base of the mountain, some butterflies circled around the mountain and returned over the top from the northeast. As they approached the old colony, these butterflies reformed clusters on trees upslope from the old colony, and, as in the other instances, on branches exposed to the afternoon sun. Thus, the path of return from water seems to be the principal factor determining the direction of the incremental type of colony movement.

Colony Breakup

Due to seasonal warming in late February and March (Fig. 5), butterfly activity increases, and the colonies begin to reverse the consolidation process as larger and larger numbers fly out to water and nectar sources. The increasing daily efflux results in an acceleration of downslope or down-canyon movement. Often the colony splits into two or more parts as the butterflies returning from daily activities reform clusters nearer water or nectar (Fig. 3d–f). As occurs when they first arrive in November, new clusters form on the periphery of branches, while interior branches and trunks are largely avoided, resulting in a lower density but an increase in the total area occupied by the colony (Fig. 3e–f). After mid-March, colony size decreases as the butterflies start their remigration northward.

The Formation and Breakup of a Colony—a Case Study

The most detailed studies of the overwintering butterflies have been conducted near Site Alpha (Brower et al. 1977), located in what we now call the Chincua overwintering area. The Chincua Area is located at 19°41′N and 100°17–18′W in the Sierra Chincua 5–7 km NNW of

FIG. 4.   Packing of monarch butterflies on trunks of the oyamel fir (*Abies religiosa*) is especially noticeable after winter storms when butterflies dislodged from their clusters by storm action crawl up the trunks.
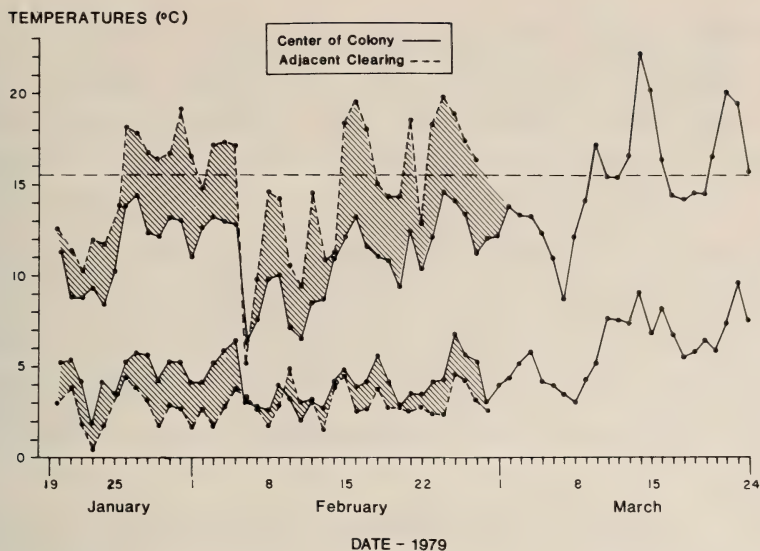
FIG. 5. Daily minimum and maximum temperatures as measured by one thermograph beneath the forest canopy in the center of a Chincua colony (Colony 10, Table 1) from 19 January–24 March 1979 (dashed lines), and another in a nearby clearing, from 19 January–28 February (solid lines). Horizontal dashed line is at 15.5°C, the approximate temperature at which monarchs are able to raise their thoracic muscles to flight temperature by shivering.

the town of Angangueo, Michoacan (Anon. 1976a: topographic map). The terrain is dominated by a SE–NW ridge of the Sierra Chincua, which drops from 3300 m to 2600 m elevation in its 6.3 km length, and is centered on a local landmark known as the Mojonera Alta ("high dividing line," Santamaria 1974). To the south, the ridge falls off steeply into the deep canyon of Arroyo La Plancha (also known locally as the Arroyo Hondo). The north slope of the Sierra Chincua is dissected by canyons that drain northwesterly. At its western end, the ridge divides forming the eastern and western sides of the westernmost of these canyons, Arroyo El Zapatero. Here butterfly colonies formed in seven of the past ten years, from 1976/1977 through 1985/1986.

We monitored the formation, consolidation, and breakup of one of these colonies (colony 10, Table 1) during the 1978–79 overwintering season (Fig. 3). When located on 15 November it was on the SW-facing slope (230°) of the head waters of Arroyo El Zapatero, approximately 140 m from the ridge crest and 180 m from the canyon bottom (Fig. 3a). At this time, the colony was still in the aggregation phase, and occupied 2.51 ha. By 13 December (Fig. 3b), it had moved downslope approximately 70 m and occupied 3.29 ha, the largest area it

would attain. By 15 January (Fig. 3c), it had moved 110 m downward and westward. Due to increased packing on trunks and the interior parts of branches, it had consolidated to 2.25 ha. On 9 February (Fig. 3d) its size had not changed, but it had moved slightly westward (20 m) with its lower and upper boundaries remaining fixed. We mapped the colony again on 3 March (Fig. 3e), by which time the butterflies were very active. The colony had split into two parts and had spread out along Arroyo El Zapatero. It now occupied a total of 2.72 ha and was located 140 m west of its February position. We mapped the colony the last time on 22 March. By then it had spread out over 1 km of the canyon, occupied 3.2 ha, and consisted of two adjacent groups (Fig. 3f) and a third group farther downstream. On 15 April, walking the entire length of Arroyo El Zapatero, we encountered only one live butterfly where less than a month before there had been tens of millions.

Colony Location in Relation to Slope Exposure

The distribution of facing azimuths of the colonies is shown in the circular diagram (Fig. 6). The mean vector was 230°18' with a 95% angular confidence interval of ±28°. Sixty-seven percent of the colonies formed on slopes in the SW quadrant, which shows a clear preference of the butterflies for this quadrant (r = 0.56, P < 0.001). Of the nine colonies that formed on slopes facing other directions, two were located just to the east, and in the lee of, a SW-facing ridge (Colonies 1 and 2, Table 1), five were located in canyons that drained to the west (Colonies 3, 5, 25, 27 and 28) and the remaining two formed on slopes facing SSE, one very close to the SW quadrant (Colonies 22 and 30). One colony formed initially on a SSE slope and later moved around to a slope in the SW quadrant (Colony 8).

During the winter in mountainous areas, southern slopes receive more insolation and dry faster than northern ones. Moreover, SW slopes are heated more than SE ones because, when the sun strikes the eastern slope in the morning, much of its energy is spent in evaporating water that precipitated as dew during the night. In contrast, the afternoon sun strikes relatively dry ground, so most of its energy is spent in heating the surface (Geiger 1950). In spite of a strong need for the butterflies to stay cool, conserve fuel, and avoid desiccation, they appear to choose the hottest and driest slopes available. This apparent contradiction needs explanation.

We hypothesize that their location on SW-facing slopes is a compromise that satisfies several requirements. During mid-winter days, air temperatures within the shade of the oyamel forests rarely become warm enough for monarchs to fly spontaneously. The minimum am-
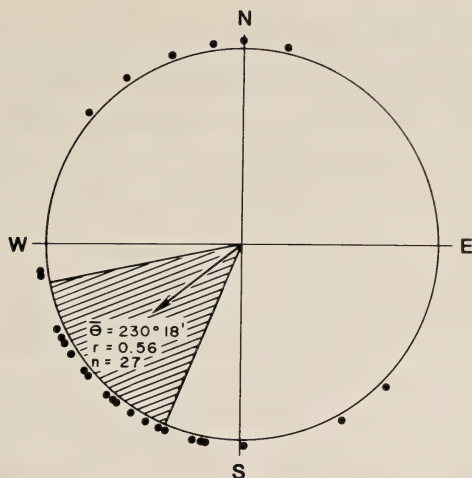
FIG. 6.   Direction of the slopes (faing azimuths) on which 27 monarch butterfly colonies were located in Mexico's Transvolcanic Belt, 1976–82. Shaded area is angular confidence interval.

bient temperature at which monarchs can shiver and then fly is between 12.7 and 16°C (Kammer 1970, Masters 1985). Air temperatures of this magnitude were not reached in shaded portions of the 1978–79 Chincua 4 colony until March 9 (Fig. 5). Even though temperatures are below flight threshold within the colony during most of the overwintering season, direct solar radiation usually reaches the butterflies as sun flecks at some time during clear or partly cloudy days. This allows them to warm to flight threshold by basking so they can regain their positions in the trees after being knocked down by storms, and also insures that they can fly out to water and nectar on clear days. In addition, their basking posture readily displays their aposematic coloration and helps to deter bird predators, which killed an average of 15,000 butterflies/day during 1978–79 (Brower & Calvert 1985). This same study showed that predation is inversely related to temperature and suggests that the birds would have an even greater advantage on the colder, north-facing slopes. Although a position on the north-facing slope would be better for maintaining water balance and conserving lipids, the colder temperatures would result in greater inactivity so that the butterflies would be less able to redress an unfavorable water balance, reestablish colony integrity after storms, avoid predators, and obtain nectar.

The Importance of Slope Inclination

Surface heating of mountainous areas depends on the amount of radiation striking slopes. While several factors including season, time

of day, latitude, and the facing direction of slope affect radiation, the degree of slope is critical. Schubert (in Geiger 1950) showed that during winter, a south slope inclined at 23.5° receives 9% more heat than a horizontal one. The inclination of the slopes on which the butterfly colonies are situated averaged 25°22′ with a 95% angular confidence interval of 1° (Table 1). Butterflies roosting here would receive more solar energy to warm them, and their ability to fly would thus be enhanced.

Moreover, surface heating due to solar radiation striking near the perpendicular to the mountainous slopes occupied by the colonies is maximal on about 1 March. This coincides well with the date that the butterflies begin to accelerate flight activity and mating, and move down the canyons in preparation for their remigration to the north. The reason for this early March maximum is as follows: At the latitude of the overwintering colonies (ca. 19.5°N), the date when the sun's rays are exactly perpendicular to the average colony slope (25°22′ = approximately 25.4°) is 1 March. At the spring equinox, the angle of incidence of the sun at the latitude of the colonies is 95.5°. This value is obtained by adding the average slope inclination (25.4°) to the angle of incidence of the sun's rays to the horizontal $[25.4° + (90° - 19.5)] = 95.9°$. Therefore, at solar noon on 22 March, the sun is 5.9° beyond the perpendicular to the average colony slope. Since the earth precesses at a rate of 0.2575°/day, it takes about 23 days (5.9°/0.2575°/day = 22.9 days) to reach this position. Therefore, the sun's rays were perpendicular to the colony slopes about 1 March.

Why Do Monarchs Migrate to Mexico's Transvolcanic Belt?

Evidence that monarchs are not sufficiently cold-tolerant to survive winter conditions in their northern breeding areas derives from several sources. Urquhart (1960) found that 77% of monarch pupae subjected to freezing temperatures associated with a cold front perished. Calvert and Brower (1981) showed that 60% of monarchs wetted by naturally occurring dewfall in a clearing near a Sierra Chincua colony suffered flight impairment or death after one night's exposure to temperatures averaging only −1.7°C. Moreover, during January, 1981 within a Sierra Chincua colony (Colony 24, Table 1) inclement weather with low temperatures reaching −5°C resulted in the death of an estimated 2.5 million butterflies (Calvert et al. 1983). Anderson (in Brower, in press) found in a controlled freezing chamber that the temperature at which 50% of the dry and wet monarchs freeze from a Chincua colony is −7.8°C and −4.4°C, respectively. Calvert et al. (in press) found in the same area that the temperature at which 50% of monarchs wetted by nighttime dewfall in the open forest freeze or are injured to the

point where they could not fly normally is −3.1°C. Thus, temperatures slightly below freezing kill or incapacitate monarch butterflies, necessitating their migration from their northern breeding grounds. An additional reason for migrating southward is the senescence of their larval food plants. However, if the monarchs could survive the cold, they could, presumably, overwinter in the north as do other adult butterflies such as the mourning cloak (*Nymphalis antiopa* L.).

The monarchs' need to avoid lethally cold temperatures must be balanced against their need for moderate cold to avoid too rapid depletion of their lipid reserves (Tuskes & Brower 1978, Chaplin & Wells 1982, Brower 1985, Walford & Brower, in prep.). Long-term minimum temperature records (10–29 years) for November through March at seven meteorological stations above 2500 m located near the overwintering colonies averaged 2.3°C (Anon. 1976b). The average minimum, average maximum and mean temperatures for a 40-day period (19 January–28 February 1979) in a clearing 20 m outside a Sierra Chincua colony (24, Table 10) were 2.9°, 14.9°, and 8.9°C (Fig. 5; also Brower & Calvert 1985). The overwintering areas are thus located at an altitude and latitude that normally provide a cool environment with relatively stable minima at or just above freezing.

The dense forests of the Transvolcanic Belt also play an important role in moderating the climate by reducing daily temperature extremes. Thus, inside the center of the colony for the same 40-day period described above, the average minimum temperature was higher (4.2°) while the average maximum and mean temperatures (11.0° and 7.7°) were lower than the corresponding averages in the nearby clearing (compare Fig. 5). The moderating effect of the forest cover becomes crucially important for monarch survival when temperatures plummet to the killing threshold (Calvert et al. 1983).

Latitudinally, the monarch's choice of colony location may be limited by two physical barriers. Immediately south of the Transvolcanic Belt lies the Balsas River depression (Fig. 1). Here the hot, dry climate would undoubtedly break their reproductive diapause (Baker & Herman 1976), and cause them to begin ovipositing in areas already occupied by indigenous milkweed butterflies, *Danaus gilippus* L. and *D. eresimus* Cramer, as well as nonmigratory monarchs (Calvert, unpubl. obs., Brower 1985). To the north lie the dry plains of the Central Plateau where in winter the butterflies would be subjected to colder and drier conditions brought about by the influence of advective air masses moving down from the north (Zepeda 1941, Mosino Aleman & Garcia 1973). In this thinly forested region they would also not have the protective cover and microclimatic requisites provided by the dense forests of the Transvolcanic Belt. Suitable habitats may exist further

south in Mexico and Guatemala, but areas above 3000 m are more limited in extent and lack the extensive fir forests found in the Transvolcanic Belt (Calvert & de la Maza, unpubl. obs., Anon. 1981: distribution of oyamel forests).

The conflicting requirements to avoid freezing temperatures and yet remain relatively cool, and to avoid excessive moisture that raises the temperature at which freezing injury occurs, and yet to remain relatively moist to avoid desiccation are closely approximated in the oyamel forest ecosystem at the geographic location between 19 and 20°N in Mexico's Transvolcanic Belt.

The monarchs' return to the north is also bounded by several constraints. It must not precede the flush of spring milkweeds and the recession of lethally cold, late winter temperatures. And finally, it must allow for the first spring generation, largely produced in the Gulf Coastal States (Brower et al., in prep.) to mature before the advent of lethally warm summer temperatures in the southern United States (Malcolm et al. 1987).

CONCLUSIONS

Monarch migration to and colonization of high altitude tropical areas in Mexico appear to be an adaptive response to several temperature- and water-related needs. Flight capacity is necessary to regain position in clusters following storms, to avoid predators, to locate nectar sources, and, especially, to obtain water. Direct and indirect solar radiation augmented by a SW exposure and favorable slope inclination allow the butterflies to warm sufficiently to fly when temperatures within the forest are below flight threshold. However, warming and flying in the course of daily activities increases their utilization of precious lipid reserves. The generally cool climate with sufficiently intense sunshine to allow flight appears to satisfy both their need to conserve energy and fly out of the colony when necessary. The location of the mountains is far enough south to minimize the impact of most cold air masses, which dominate winter weather in the north. Nighttime minima, which seldom drop more than a few degrees below freezing except during occasional extreme cold periods, reduce the likelihood of death by freezing. These often conflicting requirements are approximately satisfied by the unique climatic and physiographic features of Mexico's Transvolcanic Belt.

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A NEW *EUCHLOE* (PIERIDAE) FROM NORTHWESTERN MEXICO

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ABSTRACT. A new species of *Euchloe* related to *Euchloe ausonides* was discovered at a mountainous desert scrub locality in Sonora, Mexico. This butterfly is described from four males and compared with *Euchloe ausonides*, its close relative; no females are known. Its habitat and evolutionary significance are treated.

Before the discovery reported here, four species of *Euchloe* Hübner were known from the Americas—the most recently described being *E. hyantis* and *E. olympia,* both described by William Henry Edwards in 1871. More recent study has elucidated the systematic position, distribution, early stages, and biological features of these four species (Opler, 1966a, b, c, d, 1970, 1971, 1974, Opler & Clench 1983).

The discovery of a new *Euchloe* species by Richard Holland of Albuquerque, N.M. in northwestern Mexico was quite unexpected. The species is a member of Ausonides Species Group.

Euchloe guaymasensis Opler, new species

Male. Forewing length 19.0 mm (range 17.4–19.4 mm, N = 5). *Head.* Labial palpi covered with white appressed scales, long stiff white and black hairlike setae directed laterally and ventrally; frons with long white and black setae; vertex with mixture of yellow and a few black appressed scales; antennae 0.07 cm long, white-tipped, otherwise covered with a mixture of white and black scales, predominantly the former, inner surface of shaft and nudum naked. *Thorax.* Clothed dorsally with quadrate black appressed scales and fine long white hairlike setae; laterally and ventrally clothed with yellow appressed scales together with long white hairlike scales; legs covered mainly with white and a few black scattered scales. *Forewing.* Apex rounded with stem R4+5 much shorter than R5; dorsal surface ground pale lemon yellow, with white along costal margin from base to apex; white diffusely along inner margin; very fine white hairlike scales especially at base and along inner margin; black patch at end of discal cell concave outwardly, 9 scale rows in width with 12–14 included scattered white scales; black patch at apex dense with few included yellow scales; oblong patch (rounded in several paratypes) of pale yellow scales on costal margin between R1 and R3; fringe at apex black except for three areas with long yellow hairlike setae; few scattered appressed black scales at base; ventral surface pale yellow; small greenish patches (composed of appressed yellow and black scales) where R1 meets costal margin and where M2 and M3 meet outer margin; patch at end of discal cell of black scales with included gray white scales. *Hindwing.* Dorsal surface ground pale lemon yellow, some white along inner margin, a few appressed black scales at base; long fine pale hairlike scales especially on base and along inner margin; a few (5–15) scattered black appressed scales at endings of veins (except SC and Anals); fringe of long fine yellow hairlike scales except for a few long black scales at vein endings as above. Ventral surface ground white; marbling pattern similar to that of *E. ausonides* but with fewer connections between patches of yellow and black scales; very long (0.6 cm) "green" patch within and parallel to interior margin of discal cell. *Abdomen.* Covered dorsally and laterally with black appressed scales, a few scattered yellow or white scales inter-
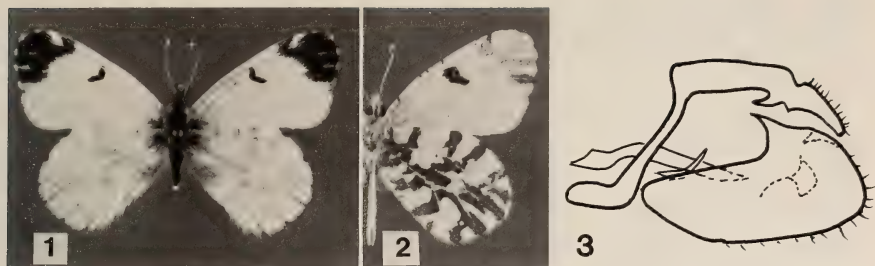
FIG. 1.   Holotype male *Euchloe guaymasensis*, dorsal view.
FIG. 2.   Paratype male *E. guaymasensis*, ventral view.
FIG. 3.   *Euchloe guaymasensis* male genitalia, lateral view.

mixed; ventrally with mixture of quadrate white and yellow appressed scales, covered with medium length white hairlike scales. *Genitalia.* As in *Euchloe ausonides* except saccus more regular in outline; cucullus areas of valvae only slightly produced after distal teeth; juxta only weakly chitonous, only dorsal arms visible.

Types. Holotype ♂, Mexico, Estado de Sonora, Las Avispas microwave relay, 2000′ (655 m), 40 mi (64 km) N Guaymas, 24 March 1983, leg. Richard Holland; genitalia preparation PAO 354 (P. A. Opler). Paratypes. Same locality, 4 ♂♂; 12 March 1974, 23 March 1983 (2), 5 March 1984; all leg. Richard Holland (the 1974 paratype with G. S. Forbes). Holotype deposited in National Museum of Natural History, Smithsonian Institution, Washington, D.C. One paratype each in collections of American Museum of Natural History, New York; Allyn Museum of Entomology, University of Florida; Los Angeles County Museum; Instituto de Biologica, Universidad Nacional Autonoma de Mexico.

The name is masculine and refers to Guaymas, the nearest city to the type locality.

COMPARATIVE ANALYSIS

Among the four previously described *Euchloe*, *E. guaymasensis* is most closely allied to *E. ausonides* (Lucas); the two species share the following characters: (1) antennae with black and white scales, (2) white scattered scales within forewing dorsal discal cell black patch, (3) lack of opalescent white scales on ventral hindwing, (4) marbling pattern on ventral hindwing neither heavy and fractured nor strongly reduced, (5) cucullus extending slightly beyond distal tooth, (6) juxta V-shaped, and (7) sterigma evenly curved in lateral view. Opler (1971) illustrated these character states, some of which—but not all—are also shared by either *E. creusa* (Doubleday) or *E. olympia* (Edwards) or both. Compared to *Euchloe ausonides*, *E. guaymasensis* differs in the following features: (1) antennae with a greater proportion of white scaling, (2) forewing more rounded at apex, (3) black patch at apex darker, without intermixed white scales, (4) forewing costal margin without black scaling, (5) ground color of both dorsal wing surfaces pale lemon yellow (usually cream white in *E. ausonides*), (6) forewing stem R4+5 much shorter than R5, (7) black scaling areas at bases of

both wings much more restricted, (8) green marbling patches on ventral hindwing less interconnected, and (9) male genitalia with juxta less chitonous.

Habitat at type locality: photographs taken by Richard Holland at the type locality show rocky, extremely rugged, mountainous terrain with a mixture of subshrubs, succulents, and woody microphyllous deciduous vegetation. Specific plants include ocotillo (*Fourquieria*), *Acacia*, and possibly *Encelia*. The type locality is clearly within the Lower Sonoran life zone.

Surprisingly, the closest nearctic relative of *Euchloe guaymasensis* is *E. ausonides*, a species of much more temperate climes, not *E. hyantis*, a butterfly of more austral habitats, including northern Sonora, Mexico. The closest localities to the *E. guaymasensis* type locality where *E. ausonides* occurs are the Kaibab Plateau, Coconino Co., Arizona, 975 km to the north, and the Sangre de Christo Mountains, San Miguel Co., New Mexico, 965 km to the northeast.

Likely it will be found elsewhere in the coastal ranges of Sonora when someone penetrates this physically intimidating habitat.

Euchloe guaymasensis differs in sufficient characters from *E. ausonides* to indicate that it has been long isolated, probably since at least the middle Pleistocene. The nature of the larval and pupal characters, when discovered, should help confirm this hypothesis.

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PHYSICAL CONSTRAINTS OF DEFENSE AND RESPONSE TO INVERTEBRATE PREDATORS BY PIPEVINE CATERPILLARS (*BATTUS PHILENOR*: PAPILIONIDAE)

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ABSTRACT. The responses of pipevine swallowtail caterpillars (*Battus philenor*: Papilionidae) to simulated attacks of invertebrate enemies and to actual attack by coccinellid larvae (*Hippodamia convergens*: Coccinellidae) were examined. The caterpillars were more reactive to the simulated attack of a biting predator than to the simulated touch by an insect enemy. Active fifth instars reached around to the posterior or walked away in response to stimuli, whereas prepupal fifth instars were more likely to extrude the osmeterium and never moved away from the stimuli. Caterpillars that were larger than the coccinellid predators were attacked but seldom eaten. In contrast, larvae that were the same size or smaller than the coccinellids were killed more frequently. When the caterpillars were attacked posteriorly, they defended a limited area by reaching around while the prolegs remained attached. The area defended depends on cuticular stretch, number of attached prolegs, current physiological state, and type and degree of stimulation.

A common view of insects as prey is that behaviorally they are rather defenseless. Dixon (1973) stated, "The general impression conveyed by the literature is that aphids and related small insects are helpless, sedentary and thin-skinned creatures that invite the attention of any predator that comes along." Generally, that same view is held for caterpillars and other immature insects. Yet caterpillars can and will defend themselves under certain circumstances, such as when attacked by insect predators and parasitoids. However, as I show here, pipevine swallowtail caterpillars (*Battus philenor* (L.): Papilionidae) have important constraints that limit the effectiveness of defensive behavior.

Most six-legged insects can turn up to 360° in their own defense. For instance, aphids can move forward or backward rapidly, and they can kick their adversaries (Banks 1957). Aphids can escape just before contact or immediately afterward by simply moving away quickly; many invertebrate predators must be within a centimeter of, or bump into, prey before detecting them (Russel 1972). Furthermore, before or after contact by predators, aphids can swivel on their stylets up to 180° and thus continue feeding while avoiding their enemies (Russel 1972, Brown 1974). In contrast, caterpillars have a cylindrical body with short thoracic legs anteriorly and short prolegs posteriorly. This means that they differ greatly in their maneuverability from six-legged insects, especially aphids which are pear-shaped with relatively long legs. As a consequence of the mobility of six-legged insects, most invertebrate predators are more mobile than caterpillars and can outmaneuver them.

Thus, caterpillars may benefit by escape, often dropping off their host plant (Myers & Campbell 1976). However, leaving the host plant can be risky. Caterpillars (and other soft-bodied insects) may starve before they locate a host plant, or die from desiccation or ground predation (Dethier 1959, Roitberg & Myers 1978, Rausher 1979). Larvae may drop on a thread of silk, which they can later climb, returning safely and quickly to their host plant (Dempster 1971). But predatory ants may climb down silk threads to capture larvae (Allen et al. 1970).

Some caterpillars feed in hiding, a strategy that appears to be especially effective for early instars (Allen et al. 1970, Lopez et al. 1976). Web-making caterpillars may disappear into their webs when disturbed (Fitzgerald 1980). But webs do not deter some wasps and pentatomids from pursuing caterpillars within (Morris 1972, Schaefer 1977). Carabid beetles may tear open webs (Langston 1957). Chrysopid larvae with their long, sicklelike mandibles, and pentatomid and reduviid bugs with their long beaks, can attack prey through cloth and webbing (Fleschner 1950, Bornemissza 1966, Allen et al. 1970, Berisford & Tsao 1975). Furthermore, some predatory pentatomids and spiders live in webs of caterpillars (Morris 1972, E. W. Evans, pers. comm.).

Therefore, caterpillars may benefit by vigorous defense when escape is less effective or more risky, such as when an insect predator initiates contact but cannot overwhelm the caterpillar. Typically, a defensive caterpillar attaches firmly to the substrate with the prolegs, lifts the thoracic legs and swings the anterior of the body toward the attacker, especially when approached from the side or rear by a predator. Caterpillars may use their bodies to hit and their mandibles to grasp an attacker (Morris 1963, McFadden 1968, Iwao & Wellington 1970, Frank 1971, Heinrich 1979, Suzuki et al. 1980, Stamp 1982). Unlike vertebrates and adult insects, caterpillars do not use their legs defensively. Instead, they may regurgitate or wipe offensive glands on attackers (Eisner & Meinwald 1965, Feltwell 1982).

The questions posed in this study were: 1) when does a caterpillar opt to escape or for defense? 2) how does it defend itself? and 3) how effective is it in defending itself, or when are insect enemies successful in countering a caterpillar's defense?

METHODS

Pipevine swallowtail caterpillars were used because of their variety of defensive responses: thrashing with the front half of the body, grasping with the mandibles, regurgitating, and extruding the osmeterium and wiping it on attackers. On 16 May 1983, eggs were collected at Rancho Cordova, California, along with Dutchman's pipevine (*Aristolochia californica* Torr.), the host plant. Caterpillars were reared in

the laboratory at room temperature in plastic boxes with the host plant stems in aquapics.

Response to Simulated Attack

To examine the responses by swallowtail caterpillars, I used two stimuli. On first, second, third, and fifth instars, a two-haired brush simulated the touch of an insect predator (palpitating antennae or beak of predatory hemipteran) or parasitoid (palpitating antennae or probing ovipositor). The stimulus was applied three consecutive times to the posterior of each caterpillar at 15 sec intervals for up to 6 trials. For the fifth instar, a pinch with forceps on a fleshy tubercle at the rear end at 15 sec intervals simulated the bite of an insect predator, such as an ant. Responses were recorded with a video camera. Thrashing with the front half of the body, biting with the mandibles, extruding the osmeterium, and regurgitating were classified as stationary defense. Walking away and wriggling (rolling around with no legs attached) were classified as escape behaviors. For Chi-square analyses, the Yates correction for continuity was used when $v = 1$, and is denoted by χ_c^2 (Zar 1974). The power of tests (probability of not committing a type II error, $1 - \beta$) was calculated as described by Cohen (1977).

To compare active and inactive larvae, the stimuli were applied in the same manner as above to two sets of final instars: feeding and prepupal (no longer feeding and residing on a silk mat).

Tests with Invertebrate Predator

To determine how effective swallowtail caterpillars were in defending themselves, they were tested with coccinellid larvae (*Hippodamia convergens* Guerin-Meneville). Coccinellid larvae are voracious predators of eggs and small insects (Banks 1957, Brown 1974). I observed a third instar *H. convergens* feeding on a second instar *B. philenor* in a riparian area in Rancho Cordova; it is thus reasonable to assume that the coccinellids are natural predators of these swallowtail caterpillars. Fourteen third instar coccinellids were collected on 23 May 1983 at Rancho Cordova, California, in a large field that had no *Battus philenor* caterpillars or host plants. Thus, the predators would not have had any prior contact with pipevine swallowtail caterpillars.

Each coccinellid was kept in a Petri dish with a source of water but no food for 24 h. Using a paintbrush, I placed each coccinellid in a Petri dish with a swallowtail caterpillar on a leaf of the host plant. Caterpillars were used only if they were actively feeding. Fluon (polytetrafluoroethylene from Imperial Ltd., England) was painted on the sides and bottom of the dish to prevent the coccinellids from searching there. The interactions of each coccinellid and caterpillar were moni-

tored for 10 min. Only those trials where the coccinellids exhibited foraging behavior were used for analysis. Some coccinellids were used more than once but only at 24-h intervals. To determine the body-size ratio (BSR), body length of caterpillars was measured in mm when they were eating and when the dorsal midline (anterior to posterior) was straight. Body length of the coccinellids was measured when they were between foraging bouts and thus motionless.

Modelling Defensive Space

The area defended by swallowtail caterpillars was determined by using a video camera to record the path of the head in response to stimuli (two-haired brush or forceps) applied to the posterior. Measurements were made from tracings of body length at the start, and how close the head came to the posterior during defense. Using a map meter, measurements were also made of body length (down the midline) when the caterpillar reached around to defend itself. Body extension was estimated by maximal body length during defense divided by body length at the start. Only the recordings where the head moved laterally rather than over the back were analyzed. While the camera recorded body movement, I recorded the number of prolegs detached immediately after the stimulus.

RESULTS

Response to Simulated Attack

In response to the two-haired brush (simulating the touch of an invertebrate predator or parasitoid), all of the tested instars exhibited escape and defensive behaviors (Fig. 1). With repeated stimulation, the larvae were more likely to exhibit escape behaviors, except for the fifth instar where the escape response declined. Defensive responses decreased with the sequence of stimuli. The fifth instar appeared to become more tolerant of the stimuli in that both defense and escape responses declined with the sequence of stimuli (Fig. 1).

Comparing responses of the fifth instar to the two stimuli showed that they were more reactive, by exhibiting responses, to pinching than to touching by the brush (χ_c^2, $P < 0.025$). But the larvae responded with escape and defensive behaviors in similar proportions (escape, defense or no response; χ^2 test, $v = 2$, $P > 0.10$, $1 - \beta = 0.58$ for $\alpha = 0.05$, $n = 58$). They were more likely to reach backward in response to the forceps than to the brush (χ_c^2, $P < 0.025$). The caterpillars also walked farther away in response to pinching than to touching by the brush (moving more than 2 cm within 15 sec or not, χ_c^2, $P < 0.05$).

Comparisons were made of behavior of active (still feeding) and

Percent of
larvae

FIG. 1. Reaction by swallowtail caterpillars to a two-haired brush touching the posterior at intervals of 15 sec (indicated by the series of numbers on the x-axis). Sample sizes were n = 9 for the first and second instars (I1, I2), n = 11 for the third instar (I3) and n = 30 for the fifth instar (I5). Responses were classified as defense or escape. Some larvae exhibited both types of response at a single trial. A. Defensive responses. B. Escape behaviors.

inactive (prepupal and no longer feeding) fifth instars. In contrast to active larvae, prepupal caterpillars exhibited no escape behavior. They responded defensively to the brush in the same proportion as caterpillars still feeding (χ_c^2, P > 0.50, $1 - \beta = 0.12$ for $\alpha = 0.05$, Fig. 2). However, prepupal larvae were more likely to extrude the osmeterium than feeding caterpillars (χ_c^2, P < 0.025). Although both the active (feeding) and inactive (prepupal) larvae reached around or thrashed, the active larvae were able to reach to their posterior or to walk away, whereas the prepupal caterpillars were much less mobile and never walked away.
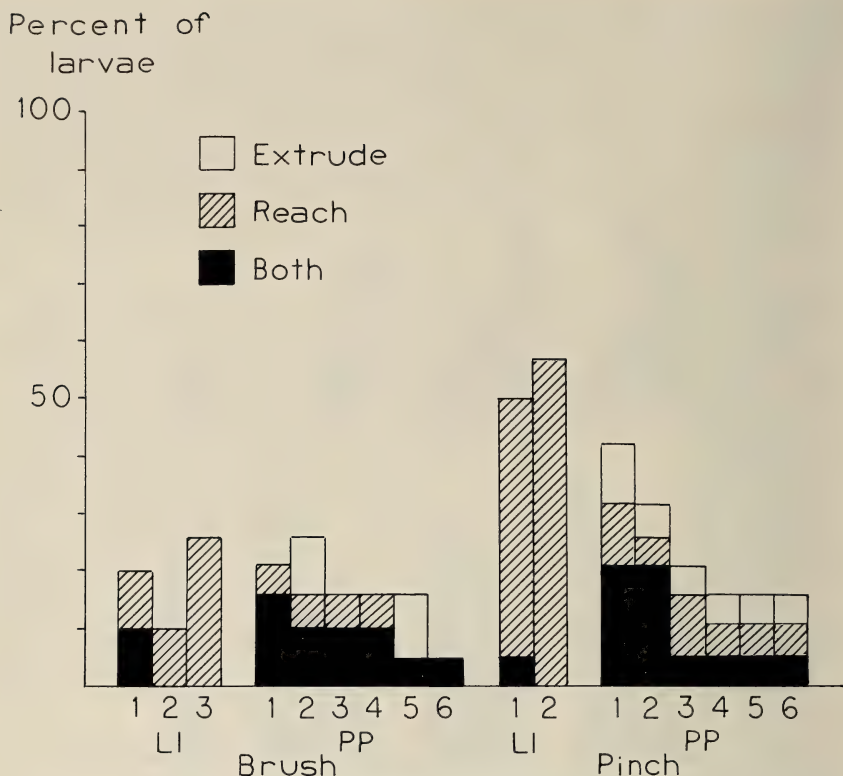
FIG. 2. Responses by active (LI—still feeding) and inactive (PP—prepupal and no longer feeding) final instar swallowtails to either a brush or forceps. Numbers on the x-axis represent the sequence of stimuli applied at intervals of 15 sec. Sample sizes were 30 and 28 for the active larvae stimulated by brush and forceps, respectively, and 35 for the prepupal larvae. Extrude—osmeterium extruded, with an attempt by the caterpillar to wipe them on the brush or forceps. Reach—caterpillar reached with head backwards toward stimulus.

Tests with Coccinellid Predators

To examine effectiveness of defense, caterpillars were monitored in response to invertebrate predators (coccinellid larvae). When the caterpillars were the same size or smaller than the predators (n = 16), 43.8% of the caterpillars were eaten. In contrast, when the caterpillars were larger than the predators (n = 16), only 6.3% were eaten. The frequencies of eaten and uneaten caterpillars were significantly different (χ^2_c, P < 0.05). Examination of the behavior of these caterpillars showed that large caterpillars (body-size ratio of prey to predator greater than 1) were more likely to thrash in response to the coccinellids, and small caterpillars (relative to the predators) were more likely to
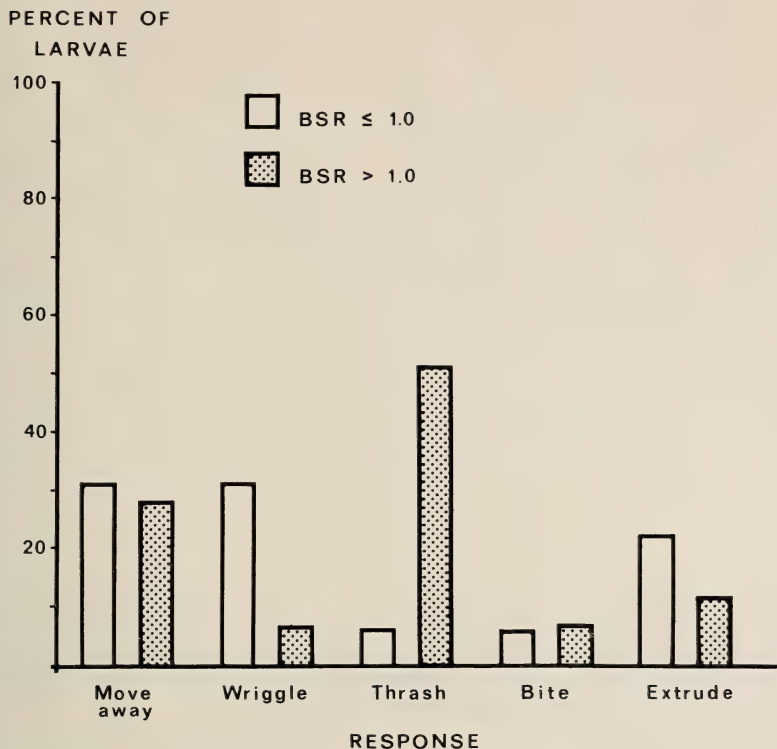
PERCENT OF
LARVAE

FIG. 3. Reaction by swallowtail caterpillars to third instar coccinellid predators. Responses are divided into those where body-size ratio (BSR) of caterpillar to predator was greater than 1, or less than or equal to 1.

wriggle (no legs attached) (χ^2 tests, P < 0.001, Fig. 3). In this experiment, body size ratio had no effect on escape, biting, or on extruding the osmeterium (Fig. 3).

Third instar coccinellids had little difficulty subduing first instar swallowtails, which were smaller than the predators. For example, after a coccinellid touched one of six first instars feeding together, the touched caterpillar extruded its osmeterium. The predator backed off, then approached and bit the larva behind its head. The other larvae had been feeding and moving around. After the first caterpillar was attacked, the rest remained motionless for 11 min. Only after the coccinellid backed into one of them did the rest leave the area. Although it took up to 15 min for a coccinellid to consume a first instar, these predators ate as many as three caterpillars consecutively. All of the coccinellids that ate pipevine swallowtail caterpillars survived and pupated, which suggests that these caterpillars are appropriate prey for the coccinellids.
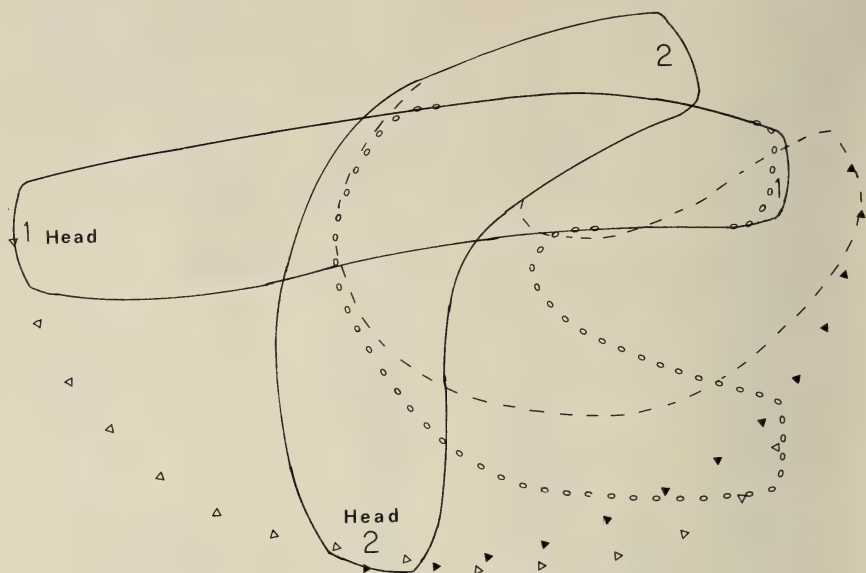
FIG. 4.   Example of typical movement of a final instar swallowtail larva in response to pinching stimuli (applied at right), based on tracing body movement from a video record. 1—position of head just before first stimulus on posterior. Open triangles show path of head after first stimulus. 2—position just before second stimulus, applied 15 sec after the first. Dark triangles indicate path of head after second stimulus.

When predator and caterpillar were of similar size, caterpillars were usually successful in defending themselves. For instance, after contact by a coccinellid, one caterpillar thrashed vigorously. The predator grabbed it. The caterpillar responded by biting the legs of the cocci-nellid but did not use its osmeterium. The coccinellid released the caterpillar, moved away, and began grooming.

Modelling Defensive Space

To determine how capable larvae were at defending their posteriors, the path of the head was traced using video recordings of larval re-sponse. As shown in Figs. 4 and 5, the caterpillars defended a limited, circular area around themselves. This was a consequence of their head-to-rear defense, where they did not turn around and place their pos-terior away from the stimulus as most animals do. Both stimuli elicited the head-to-rear response. Although some caterpillars may feed while attached to a branch, and consequently are restricted in their ability to turn around, many caterpillars are free to move around on the leaves on which they reside. Those in this study were unrestricted also. Thus,
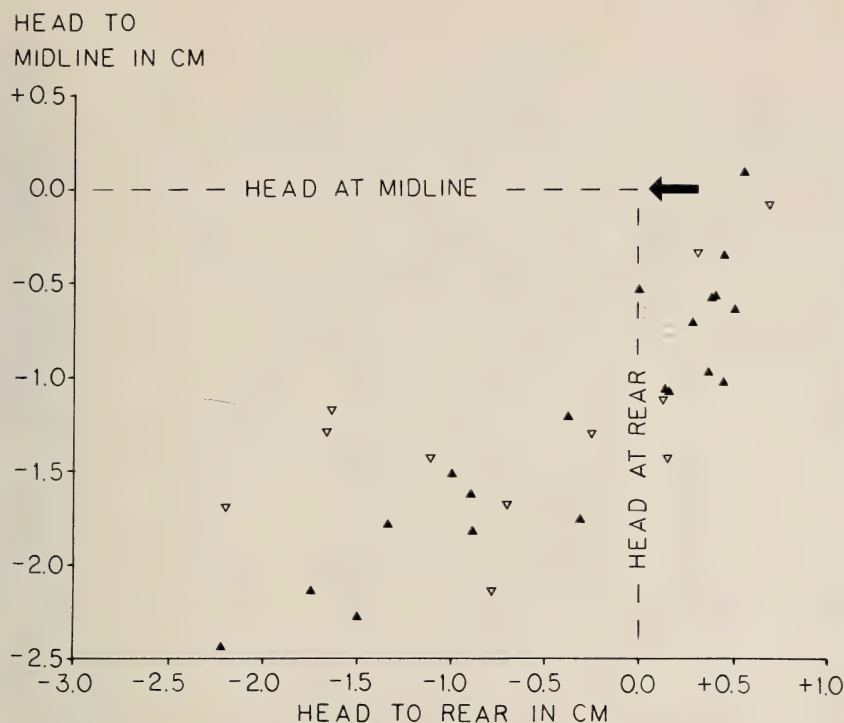
FIG. 5. Response by fifth instar swallowtails to either the two-haired brush or forceps applied to the posterior (arrow). Caterpillar's head always began at the top left and moved to the side (down and to the right). The farthest point of the head back toward the posterior is shown. Open triangles indicate response to the brush by 11 caterpillars, dark triangles the response to the forceps by 20 caterpillars.

these caterpillars exhibited a head-to-rear defense even when they could have turned around completely to face attack.

Of 31 fifth instars, 48% responded by reaching to or beyond the posterior. That so many did so was due to two factors: body extension, and detaching some prolegs. In response to the brush, body extension (beyond the original length) was 30% ($\pm$4.0 SE, n = 11). Extension was 33% ($\pm$4.5 SE, n = 20) in response to the forceps, with no significant difference between the two stimuli (arcsin transformation, two-sample t-test, P > 0.50, df = 1,29, $1 - \beta = 0.46$ for $\alpha = 0.05$). These caterpillars have five pairs of prolegs but may detach up to four of the anterior pairs in defending themselves. The mean number of attached pairs after brush stimulation was 4 ($\pm$0.3 SE, n = 11), and after pinching, 4 ($\pm$0.1 SE, n = 20, square-root transformation, two-sample t-test, P > 0.20, df = 1,29, $1 - \beta = 0.46$ for $\alpha = 0.05$).

DISCUSSION

Response to Attacks

Defensive and escape behaviors varied with instar and physiological state (active versus prepupal larvae). For example, the prepupal larvae were more likely to extrude the osmeterium than active caterpillars (those still feeding). The active larvae were mobile and thus could escape, whereas the prepupal larvae were not mobile, were slow to respond, and thus had no escape options and few defensive ones. Correspondingly, invertebrate predators and parasitoids may be more successful when attacking relatively defenseless (inactive or small) insects than when attacking active and larger ones (Dixon 1959, Evans 1976, Cate et al. 1977, Tilman 1978). For example, Rabb and Lawson (1957) stated that "an appreciable number" of tobacco hornworms captured by *Polistes* wasps were molting, and often those wasps approached but left alone fifth stage (large) larvae. Iwao and Wellington (1970) found that tent caterpillars differed in their behavior, with inactive types being less defensive and more often parasitized. Similarly, in this study coccinellid predators were more successful in their attacks when *B. philenor* caterpillars were smaller than they were.

The caterpillars defended themselves by biting the coccinellids, particularly on their legs, by extruding the osmeterium and wiping it on the coccinellids, and occasionally by thrashing and regurgitating. The caterpillars were more reactive to pinching than to touch by the brush. Probably pinching provided a clear signal of attack, whereas the brush stimulus may be received as a more general signal and not clearly different from the touch of a leaf moved by the wind. Relatively large caterpillars thrashed in response to the coccinellids; most of the time the coccinellids responded by backing off and eventually leaving the caterpillars alone. In contrast, the small larvae often wriggled when touched by the coccinellids. By wriggling, the caterpillars moved erratically, which may have made it difficult for the predators to respond effectively to the prey (Humphries & Driver 1967); some caterpillars rolled off the leaf and escaped from predators.

Physical Constraints of Defense

The premise here is that by moving only the front half of the body, the typical caterpillar defends a limited space around itself (to either side and over its back, Fig. 6). Variables that affect the maximal defendable area are: L, the length of the moving (defending) portion of the body; D, the diameter of the body; and M, the length of the moving portion of the body after maximal cuticular stretch. To estimate M, the cuticle was extended by 25% (a reasonable estimate based on Hep-
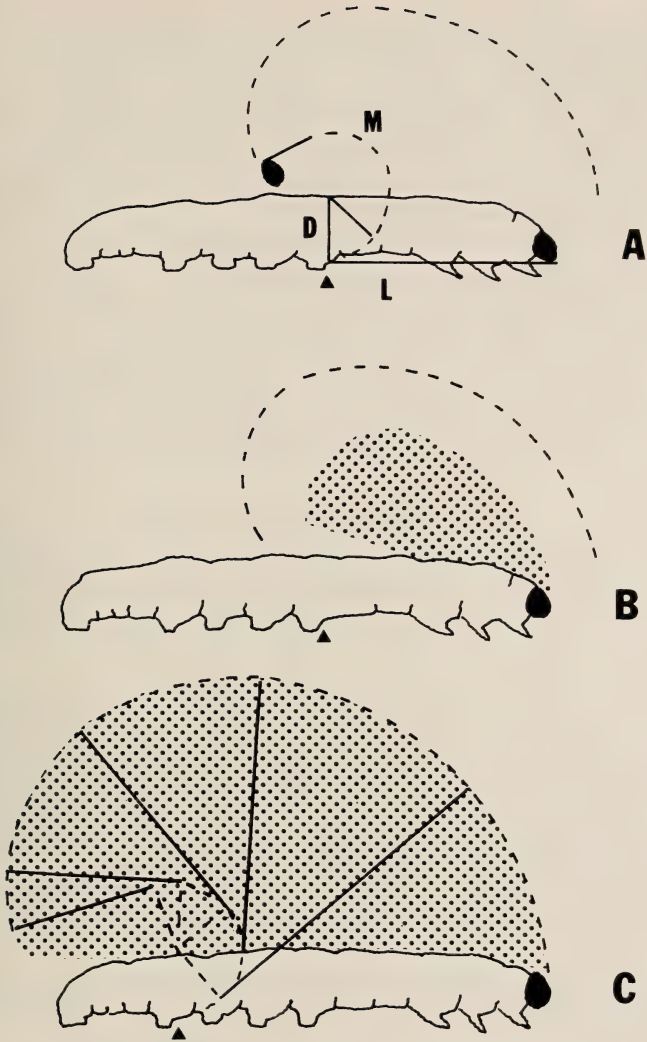
FIG. 6. A. Defendable area of a typical caterpillar when arching the head over its back. B. Shaded portion shows maximal defendable area when there is no cuticular stretch, dashed line when there is cuticular stretch. C. With only two pairs of prolegs attached, a caterpillar can defend a much larger area than depicted in A.

burn & Levy 1975, Wolfgang & Riddiford 1981, Fig. 6B). Cuticular stretch lengthens the outer bending side and thus accommodates the body volume. The effect of cuticular stretch is to increase the reach and, consequently, maximal defendable area of the caterpillar. The illustrations (Figs. 4, 5 & 6) indicate where caterpillars may be most

vulnerable to attack by insect enemies that cannot simply overwhelm them. That area is some portion of the rear end. With some prolegs detached, a caterpillar can defend a larger area and reach beyond the posterior than when five sets of prolegs are attached (Fig. 6A & C). Thus, the maximal defendable area of a particular caterpillar should affect: 1) type of defensive behavior employed by the caterpillar; 2) attack behavior of enemies, especially specialist parasitoids; 3) the sequence of attack-defense behaviors exhibited during enemy-caterpillar interactions; and 4) outcome of the event.

Using measurements of body diameter and the moving (defending) portion of a caterpillar relative to total body length, the maximal defendable space can be estimated (Fig. 6). When the ratio of the moving portion relative to total body length is high, or when diameter of the body is small, the caterpillar can reach its posterior easily (Fig. 6C). A slender geometrid caterpillar that has two pairs of prolegs uses this increased maneuverability to its advantage by preying on small insects that touch its posterior (Montgomery 1982). Cuticular elongation may also affect maximal defendable space because it allows cuticular adjustment (stretch of the outer bending surface) to accommodate a body volume that is more or less compressible, depending on how close the caterpillar is to molting to the next instar (Fig. 6B).

Most invertebrate predators rely on tactile and chemical cues more than visual ones to detect prey (chrysopid larvae, coccinellid larvae and adults, predatory wasps, pentatomid bugs; Banks 1957, Klingauf 1967, Fleschner 1950, Storch 1976, Steiner 1974, Hicks 1931, Evans 1982). Usually, such predators encounter their prey physically before they attack (Banks 1957, Dixon 1959, Swynnerton 1915, Allen et al. 1970, Myers & Campbell 1976). Consequently, predators may benefit by attacking whatever part of the prey they encounter and thus prevent the victim's escape (Brown 1974, Evans 1982).

But invertebrate predators and parasitoids often attack prey and hosts cautiously. For instance, predatory pentatomids (*Perillus circumcinctus*) tested most potential prey (chrysomelid larvae) by extending the beak and then retreating when the prey defended themselves (E. W. Evans, pers. comm.). After contact is made and prey defense is initiated, invertebrate predators may best respond to a prey's defense by attacking the most vulnerable part of the prey. For example, aphids are more likely to be caught by predators when approached from the rear (Dixon 1958, Klingauf 1967). For caterpillar-shaped animals, the posterior may be the most vulnerable location also (sawfly larvae, Morrow et al. 1976). Parasitoids that attack Baltimore checkerspot caterpillars outside the communal webs maneuver carefully toward the hind end of the defensive hosts (Stamp 1982). Consequently, the proportion

of successful assaults may be greater on the posterior than near the head.

In conclusion, when a caterpillar is smaller than the predator, the caterpillar is less likely to defend itself successfully. In this case, escape may be a more appropriate response. In contrast, when the body-size ratio of the caterpillar to the insect predator is large enough, a caterpillar's defense may be fairly effective. But caterpillars can defend only a limited space around themselves due to the particular stance they take. The maximal defendable space of caterpillars should change with body diameter, length of the moving (defending) portion of the body relative to total length, cuticular stretch, and physiological state. Insect enemies that cannot overwhelm a caterpillar may respond to the maximal defendable space by orienting to and attacking the more vulnerable (less defended) portion of the caterpillar's body.

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NATURAL HISTORY OF *GNOPHAELA LATIPENNIS* (BOISDUVAL) (ARCTIIDAE: PERICOPINAE) IN NORTHERN CALIFORNIA

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ABSTRACT.   Diurnal *Gnophaela latipennis* (Boisduval) has a protracted summer flight and is univoltine with four larval instars, the second of which overwinters. Phenology and natural history of the egg, larva, pupa, and adult are discussed relative to the principal larval host, *Hackelia californica* (Gray) Johnston (Boraginaceae), in study areas in the northern Sierra Nevada. The egg, all larval instars, and pupa are described.

Gnophaela latipennis (Boisduval) (Arctiidae: Pericopinae) (Figs. 1, 2) is common to California, Oregon, and Washington, especially in the meadows and other forest openings of the Cascade, Sierra Nevada, and Coast ranges (Stretch 1872–1873, 1882, Dyar 1900, Powell & Hogue 1979, T. D. Eichlin, pers. comm.). Stretch (1872–1873, 1882) noted its abundance in the Siskiyou Mountains and Sierra Nevada. Its range extends from Easton, Kittitas Co., Washington [U.S. National Museum record (D. C. Ferguson, pers. comm.)] to "southern California" (the Illinois Natural History Survey has a specimen labeled "Santa Monica, S. Cal., 1 May 1879"), but its current distribution does not appear to extend south of Kern Co. (Greenhorn Mountains at the southern end of the Sierra Nevada) (J. P. Donahue, pers. comm.). It has been collected as low as 244–305 m [Big Creek Nature Reserve (University of California), Monterey Co., California] but more often at elevations ranging from 396–1890 m (J. A. Powell, pers. comm.).

Gnophaela latipennis occurs in localized populations (Stretch 1872–1873) as caterpillars (Figs. 5, 6) on boraginaceous hosts: *Cynoglossum grande* Douglas ex Lehmann, *C. occidentale* Gray, *Hackelia californica* (Gray) Johnston, *Mertensia* sp., and *Myosotis* sp. (Stretch 1872–1873, 1882, Dyar 1900, Donahue 1979, Powell & Hogue 1979) and as conspicuous black and white, diurnal moths (Figs. 1, 2) that fly lazily during nectaring and oviposition. The flight behavior is similar to that of *Gnophaela vermiculata* (Grote) in the Rocky (Cockerell 1889) and Uintah mountains.

Available literature on the natural history of *G. latipennis* is scant, and little is known about its phenology. The purpose of this paper is
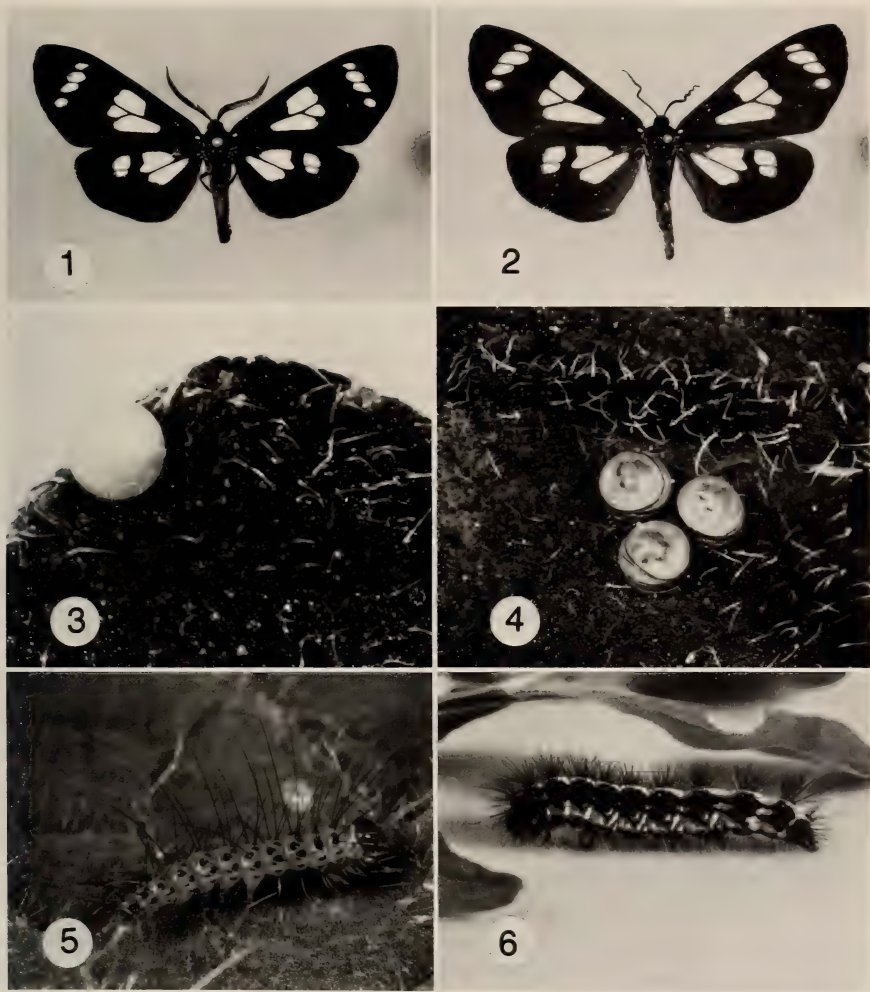
FIGS. 1–6.   *Gnophaela latipennis.* 1, adult male; 2, adult female; 3, undeveloped egg; 4, eggs ready to hatch; 5, first-instar larva; 6, last-instar larva.

to report on these matters relative to populations of *G. latipennis* in the northern reaches of the Sierra Nevada.

STUDY SITES AND METHODS

Field observations and collections focused on two areas during 1979–1983 in Plumas Co., California: Sunflower Flat, 1463 m, 4.8 km NWW of Chester; and Section 26 on Mud Creek Rim, 1676 m, 6.4 air km
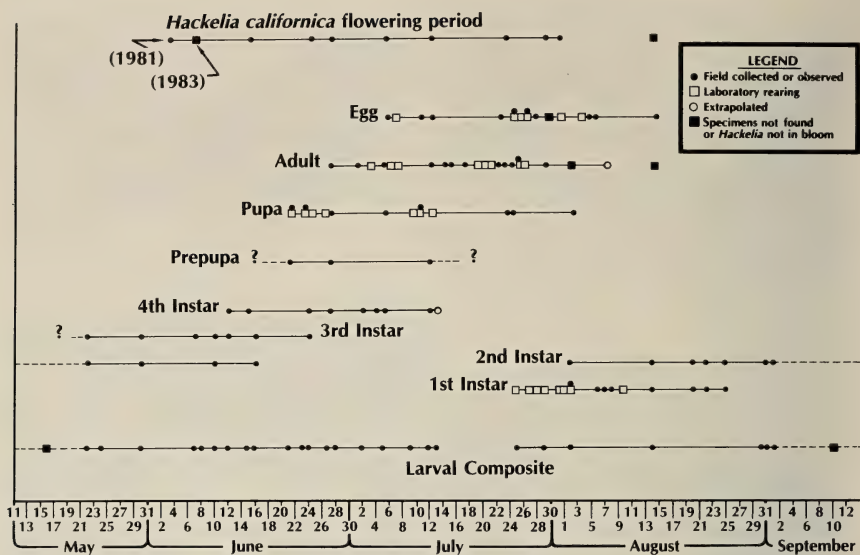
FIG. 7. Phenology of *Gnophaela latipennis* in relation to the flowering period of its principal host, *Hackelia californica*, near Chester, Plumas Co., California.

NE of Chester. Both sites are typical Sierran montane forests disturbed by earlier timber harvesting activity. The dominantly coniferous vegetation is a mixture of *Abies concolor* (Gordon & Glendinning) Lindley, *Pinus lambertiana* Douglas, *P. jeffreyi* Greville & Balfour, and *Libocedrus* (*Calocedrus*) *decurrens* (Torrey) Florin. The shrubby understory is primarily *Ceanothus velutinus* Douglas ex Hook, *Arctostaphylos patula* Greene, and *Castanopsis sempervirens* (Kellogg) Dudley. *Hackelia californica* is the most abundant herb, and *Cynoglossum occidentale* occurs infrequently. Additional observations were made in Butte Co., 11.2 air km SE (Brown's Ravine, 1585 m) and 14.5 air km SE (1890 m) of Butte Meadows. These areas are 40 air km SW of Chester.

Site examinations and observations began with receding snow cover in mid-May and continued with occasional unavoidable interruptions into September. Field data were composited into a generalized seasonal history (Fig. 7). Part of the generalization was extrapolated by determining the durations of the egg and pupal stages under ambient laboratory temperature, and by noting the hatching of field-collected eggs to establish the onset of the first larval instar.

Hinton's (1946) setal nomenclature was used in the larval descriptions.

OBSERVATIONS AND DISCUSSION

Adult. The adults (Figs. 1, 2) of *Gnophaela latipennis*, a univoltine species, exhibited a protracted summer flight period (Fig. 7). They emerged from field pupae by 27 June and were numerous and active during the first three weeks in July; but adults observed after that time appeared weak and ragged. The last field sighting of an adult during the 4-year period was 29 July. However, egg clusters were seen on three later occasions, one as late as 14 August. As the minimum hatch-time of a *G. latipennis* egg is about seven days (discussed under "Egg"), the female that laid the eggs would have been alive at least through 7 August. Thus, observed and extrapolated information indicates that adults fly between 27 June and 7 August in the Sierra Nevada study areas. In the Coast Range of California, adults have been observed as early as 25 May (8.0 air km SE Hayfork, Trinity Co.), 5 June (UC Big Creek Nature Reserve, 244–305 m, Monterey Co.), 8 June (emergence) (Buttercreek Meadows, 12.9 km W Hayfork, 1143 m, Trinity Co.), and 9 June (Kelseyville, Lake Co.) (Powell, pers. comm.).

Hackelia californica, the principal larval host at the study sites near Chester, was used extensively by adult *Gnophaela latipennis* for nectar. Its flowering period began approximately three weeks before the first *G. latipennis* adults emerged (heavy snow cover during the winter of 1982–1983 resulted in a late spring, hence the lack of blossoms on 7 June 1983) and overlapped their flight period through 31 July (Fig. 7). By the third week of July, however, most blossoms had been succeeded by well-developed nutlets. These nutlets are covered with prickles (Munz 1970), and two adults were found stuck to them on 29 July and five on 23 July 1980. *Gnophaela latipennis* also nectared at the flowers of *Cynoglossum grande* (Butte Co.), *C. occidentale*, and *Helianthus* sp. The latter, plus *Senecio*, were visited by *Gnophaela vermiculata* in the Rocky Mountains (Cockerell 1889).

Many pairs of *G. latipennis* were observed mating between 5–25 July on nectar plants, larval host plants, adjacent vegetation, and once on the end of a *Pinus jeffreyi* branch. One mating pair remained coupled for 3 h; a second pair, for 10 h.

Egg. Eggs occurred from 5–14 July (Fig. 7) and were usually found in clusters on the undersides of larval host plant leaves, as observed on *Hackelia californica* and *Cynoglossum occidentale*. However, eggs also were sporadically found on such unrelated plants as *Pinus jeffreyi* (Pinaceae) (22 eggs among needles), *Stipa* sp. (Gramineae), and *Ceanothus velutinus* (Rhamnaceae) (10 eggs on the underside of a leaf).

The number of eggs per cluster laid in the laboratory ranged from 5–13 ($\bar{x}$ = 10.3/cluster, SD = 2.6, n = 7), whereas field-collected eggs

No. of Specimens
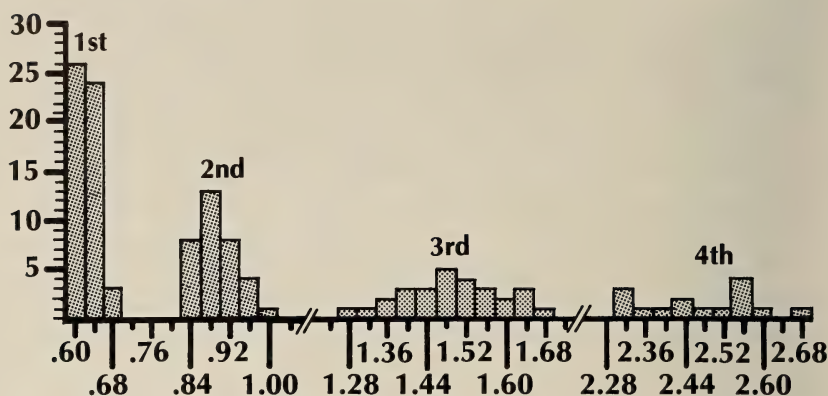
FIG. 8.   Measurements, frequency, and distribution of *Gnophaela latipennis* head capsule widths based on field-collected and reared larvae.

from larval host plants ranged from 1–21 ($\bar{x}$ = 10.0, SD = 6.5, n = 14). The egg clusters from *Pinus jeffreyi*, *Stipa* sp., and *Ceanothus velutinus* were disregarded in determining cluster size. The total egg complement of *Gnophaela latipennis* females was not fully determined, but a single female field-collected *in copula* on 5 July laid 157 eggs the following day, and a second female that emerged and mated in the laboratory produced 109 eggs.

The newly laid egg (Fig. 3) is smooth, spherical, yellow, and measured 1.25–1.32 mm in diameter ($\bar{x}$ = 1.31 mm, SD = 0.03, n = 6). Shortly before hatching, the head capsule and long, black, body setae were easily visible through the chorion (Fig. 4). The top of the egg collapsed near the head capsule. During hatching, the mandibles may be seen, under magnification, biting at the collapsed region to effect an exit hole for the larva.

Hatching time was 7–8 days; in one laboratory situation, 19 of 34 eggs hatched in seven days (15 failed to hatch) and in a second case, 37 of 38 eggs hatched between seven and eight days (1 failed). The maximum stage duration of any field-collected eggs was seven days (2 collected on 22 July 1983 hatched on 29 July).

Larva. Four larval instars were determined by the distribution and frequency of head capsule widths of field-collected and reared larvae (Fig. 8):

First instar (Fig. 5). Head capsule, width 0.60–0.68 mm ($\bar{x}$ = 0.62
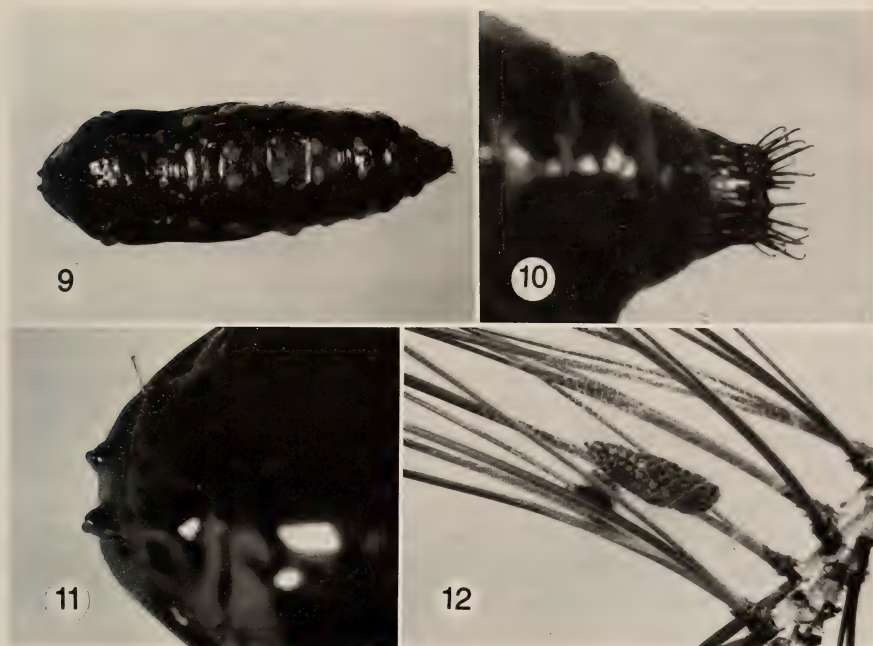
FIGS. 9–12. *Gnophaela latipennis* pupa. 9, habitus (dorsal); 10, cremaster (dorsal); 11, head tubercles (dorsal); 12, in cocoon on *Pinus jeffreyi* (head towards branch).

mm, SD = 0.02, n = 52), tan, setae translucent. Body translucent greenish yellow with distinct black tubercles on T-2–Ab-9; cervical shield yellowish tan, setae translucent, majority of D and SD setae longer than body diameter and black; L and V setae shorter and translucent; D and SD on Ab-1–Ab-8 unisetose; crochets in homoideous mesoseries. Active 25 July–25 August (Fig. 7).

Second instar. Head capsule, width 0.84–1.00 mm ($\bar{x}$ = 0.89 mm, SD = 0.04, n = 34), reddish brown, setae tan to black. Body initially concolorous with first instar but cervical shield darkens, black stripes appear, SD and D1 tubercles become slightly iridescent bluish black; D and SD setae subequal in length to body diameter, most tubercles multisetose; crochets heteroideous mesoseries. Extends from 2 August–16 June (overwinters) (Fig. 7).

Third instar. Head capsule, width 1.28–1.68 mm ($\bar{x}$ = 1.49 mm, SD = 0.10, n = 28), concolorous with preceding instar. Body yellow and black striped, tubercles iridescent blue; D and SD setae shorter than body diameter; otherwise similar to second instar. Seen from 22 May–24 June (Fig. 7). (The occurrence on 22 May indicates that some third instars may overwinter.)

Fourth instar (Fig. 6). Head capsule, width 2.32–2.68 mm ($\bar{x}$ = 2.47 mm, SD = 0.11, n = 15), reddish brown. Body concolorous with third instar. Seen 12 June–13 July; prepupae 21 June–12 July (Fig. 7).

During the study period, only three of the five borages previously mentioned had *G. latipennis* larvae on them: *Hackelia californica*, *Cynoglossum occidentale*, and *C. grande*. The latter two species were less abundant and were considered minor hosts; *C. grande* did not occur in the study sites near Chester but was present in Butte Co. *Hackelia californica* seems to be an aggressive, early successional plant that becomes abundant in areas disturbed by logging activities. Several early instar larvae may feed on the same host-plant leaf, dispersing as they grow. Negative feeding results were obtained when two groups of five first-instar larvae were placed on *Pinus jeffreyi* and *Ceanothus velutinus*, two of the "nonhosts" on which eggs were found.

The overwintering site of the second-instar larvae was not discovered. Larvae were observed feeding on *Hackelia californica* as late as 1 September, but by 10 September, no larvae could be found on this perennial or under its basal leaves or elsewhere in known feeding areas. Neither could inactive larvae be found under *H. californica* in accumulated duff and around its woody root crowns in early spring.

In 1982, spring larvae were detected feeding at Sunflower Flat on 22 May; none had been seen there six days earlier. At Section 26, no larvae were found on 16 May when *H. californica* was 2.5 cm tall and snow patches still persisted, but by 30 May, larvae were seen feeding on this host plant when it was 7.6 cm tall. Of the three larvae collected on 22 May, two were third instars, which indicates that they also may overwinter; however, none were seen in the fall.

The latest date that last-instar larvae were observed actively feeding (13 July) is one day later than the latest date for prepupae (12 July). The earliest date a prepupa was seen (21 June) coincides with the first pupal record (Fig. 7). Therefore, the prepupal time line in Fig. 7 should be extended in both directions, but there are insufficient data to determine extention lengths.

Pupa. Pupae occurred from 27 June–2 August (Fig. 7), and the duration of single pupae was 9–12 days ($\bar{x}$ = 10.5 days, n = 11) based on the pupation dates of field-collected, last-instar larvae, and the adult emergence dates.

The pupa is black with conspicuous yellow to orange abdominal spots (Fig. 9), is slightly "hairy," and ". . . suspended hammocklike . . ." (Powell & Hogue 1979) by its cremaster (Fig. 10) and two head tubercles (Fig. 11) inside a white, loose, lacelike cocoon (Fig. 12). Only two of the dozens of pupae (and three prepupae) found during this study were in *Abies concolor* foliage. Most were seen in young *Pinus*

jeffreyi at heights ranging from 1.8–3.7 m, where the cocoons had been spun solitarily among the needles. Much time was spent searching unsuccessfully for pupae in other tree and shrub species, but the absence of pupae on other vegetation or on the ground does not preclude the possibility of undetected predation. For *Gnophaela vermiculata*, Bruce (1888) noted "... when full grown the whole brood [larvae] appears to make for the nearest detached rock where they spin their cocoons in angles and crevices, generally in clusters, and often covering each others [Sic] cocoons so thickly that many of the moths are not able to make their way through but die crippled." Although one *G. latipennis* moth was seen in the field with deformed wings, obviously unable to escape from the cocoon, no general deformity problem was evident.

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GROWTH OF THE BUCKMOTHS *HEMILEUCA LUCINA* AND *H. MAIA* (SATURNIIDAE) ON THEIR OWN AND ON EACH OTHER'S HOSTPLANTS

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ABSTRACT. We compared larval growth of *Hemileuca lucina* and *H. maia* on their own and on each other's hostplants. As expected, relative growth rate (RGR) of *H. lucina* was higher on its own host (*Spiraea latifolia*) than on the nonhost (*Quercus prinoides*). Unexpectedly, RGR of *H. maia* on its own host (*Q. prinoides*) and on the nonhost (*S. latifolia*) were low and similar.

Two species of buckmoths, *Hemileuca lucina* Hy. Edw. and *H. maia* (Drury) (Saturniidae), occur in the northeastern United States. They overlap some in geographic range, but their hostplants are usually different.

Hemileuca maia is widespread but uncommon in the eastern United States, occurring from Massachusetts and Michigan south to Texas and Florida, and west to Missouri and Illinois (Ferguson 1971). It is usually associated with scrub oak, *Quercus ilicifolia* Wang. (Fagaceae), although it has been reported feeding on other oak species (*Q. laevus, Q. rubra, Q. stellata* and *Q. velutina*) (Tietz 1972). It also has been found on willow (*Salix* sp.), poplar (*Populus* sp.) and cherry (*Prunus* sp.) (Tietz 1972). Although Tietz (1972) reports *H. maia* on *Spiraea salicifolia*, this may have been a mistaken identification.

In comparison to *H. maia, H. lucina* occurs in Massachusetts, southern Maine and New Hampshire. Sometimes it is abundant, but populations are quite local and subject to large fluctuations in density. The hostplant, *Spiraea latifolia* (Ait.) Borkh. (Rosaceae), is much more widespread than *H. lucina*. The reasons are unknown, but may be linked to thermal requirements of the larvae (Stamp & Bowers 1986a). *Hemileuca lucina* has been found occasionally on *Betula populifolia, Prunus serotina* and *Quercus* sp. (Tietz 1972, Bowers & Stamp 1986).

The moths' ranges overlap in some areas of Massachusetts. For example, a population of *H. maia* occurs in pine barrens at Montague, Mass. (D. Schweitzer, pers. comm.), and populations of *H. lucina* are scattered throughout Leverett, Mass., in wet fields with *S. latifolia*. These areas are all in Franklin Co.

As with many hemileucines, these species overwinter as eggs (Tuskes 1984). The larvae feed in the spring and pupate in the soil, where they aestivate until adult emergence in the fall. Phenologies in Massachusetts are offset slightly, with egg hatch and adult flight later in *H. maia*.

The objective of this study was to compare the abilities of *H. lucina* and *H. maia* to grow on their own and on each other's hostplants. Oak leaves are relatively tough (Feeny 1970), especially compared to *Spiraea* leaves, although leaf toughness increases in *Spiraea* with leaf age (Stamp & Bowers 1986b). The leaves of these species probably differ in other important ways as well, such as in water content, and presence and amount of tannins and other allelochemicals. Because the moths are congeneric and have similar life history traits (Ferguson 1971), we expected that they could eat each other's hostplants but, because their food is different, that they would grow best on their own host species.

METHODS

For the experiment, *H. lucina* larvae were reared from an egg cluster collected on 14 April 1985 at Leverett, Mass., where the hostplant was *S. latifolia*. The egg cluster was kept in a refrigerator until 2 June; the larvae hatched on 6 June. Newly hatched *H. maia* larvae were collected from *Quercus prinoides* Willd. on 7 June 1985 at Barnard Valley (Nantucket), Mass. Caterpillars were kept in a growth chamber on a photoperiod of 16L:8D at 25°C during the day and 20°C at night, and were reared through the first instar on their own hostplants. At the beginning of the second instar, half of the larvae of each species were fed *S. latifolia* and half were fed *Q. prinoides* leaves. Larvae were given these diets throughout the second instar.

At the beginning of the third instar, the growth tests were begun with larvae fed on the same diet they had during the second instar. For each treatment, 14 newly molted, unfed larvae were weighed and placed individually in Petri dishes, with a weighed sprig of *S. latifolia* or leaf of *Q. prinoides*. Sprigs of *S. latifolia* were used because individual leaves were small and dried quickly. We used unlignified sprigs (leaves young and stems still green) because new leaves were primarily what *H. lucina* ate in the field. The larvae were given average sized *Q. prinoides* leaves. Each dish had a piece of wet toweling taped to its top to maintain humidity. Larvae fed freely for 48 h. Then they were weighed again, frozen, dried at 50°C for 72 h and reweighed to obtain wet-weight-to-dry-weight conversion factors to estimate initial dry weight. To compare the response of larvae to the two hostplants, a standard index of growth, relative growth rate (RGR), was used (Waldbauer 1968, Slansky & Feeny 1977).

TABLE 1. Growth indices for third instar *Hemileuca lucina* and *H. maia*. Each treatment had 14 larvae. Means are indicated with ±1 SE. Means with the same letter in that column are not significantly different at the 0.05 level using the Newman-Keuls multiple range test.

Diet during second instar and test period	Mean dry weight per larva (mg) at beginning of test	RGR (mg/mg larva/day)	Mean dry weight per larva (mg) at end of test
		H. lucina	
Spiraea	5.1 ± 0.2 a	0.45 ± 0.03 a	13.9 ± 1.0 a
Quercus	3.8 ± 0.2 b	0.34 ± 0.01 b	7.8 ± 0.5 b
		H. maia	
Quercus	4.6 ± 0.2 a	0.17 ± 0.01 c	6.7 ± 0.4 b
Spiraea	2.9 ± 0.3 c	0.18 ± 0.01 c	4.1 ± 0.4 c

RESULTS AND DISCUSSION

After rearing through the second instar, *H. lucina* larvae fed *Spiraea* were heavier than those fed *Quercus*, but were similar in estimated dry weight to *H. maia* fed *Quercus* (Table 1). As expected, RGR of *H. lucina* fed *Spiraea* was higher than for those fed *Quercus*. But, unexpectedly, RGRs for *H. maia* on *Spiraea* and *Quercus* were both low and similar. Because *H. maia* growth on *Quercus* was so slow, those larvae did not gain much weight during the test (Table 1). Consequently, *H. lucina* fed *Spiraea* weighed significantly more at the end of the test than larvae in the other treatments.

The relative growth of *H. lucina* on *Quercus* was probably the same as that of third-instar *H. lucina* reared on old leaves of *S. latifolia* (0.34 ± 0.01 SE on *Quercus*, and 0.35 ± 0.01 SE on old *Spiraea*; two-sample *t*-test, df = 26, P > 0.50, $1 - \beta = 0.31$ at $\alpha = 0.05$; data for old *Spiraea* leaves from Stamp & Bowers 1986b). Thus, *Quercus* and old *Spiraea* leaves were similar as food for *H. lucina*, but it was not clear why. *Hemileuca maia* did not exhibit such a pattern; it grew equally slowly on both its hostplant *Quercus* and nonhost *Spiraea*. This suggests that *H. maia* simply grow slowly in comparison to *H. lucina*. Alternately, *Q. prinoides* may be a less suitable host than *Q. ilicifolia*, the usual host of *H. maia*. However, in northern New York, *H. maia* used both oak species, and in one area used *Q. prinoides* predominantly even though the other oak species was present (Cryan & Dirig 1977).

The end result (in this case, middle of the third instar) was quite different dry weights among the treatments (Table 1). *Hemileuca lucina* fed on *Quercus* weighed but 56% of the weight attained by *H. lucina* reared on *Spiraea*. Even more striking, *H. maia* reared on its hostplant *Quercus* weighed only 49% of that attained by *H. lucina* on its hostplant *Spiraea*. Because adults of these two buckmoths are similar

in size (*H. lucina* somewhat smaller; Cryan & Dirig 1977), it seems likely that *H. maia* larvae may have a prolonged developmental period compared to that of *H. lucina*. Warrington (1985) found such an effect, with the combination of RGR and weight of prepupal larvae affecting the pupation date for four species of geometrids feeding on sycamore.

Prolonged larval development in *H. maia* may have important ramifications for exposure to abiotic conditions, predators and parasites and, consequently, for the means by which *H. maia* cope with those factors, especially compared with *H. lucina*.

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THE SPECIES OF *PSEUDEXENTERA* (TORTRICIDAE)

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ABSTRACT. Seventeen species of the nearctic genus *Pseudexentera* are recognized based on sometimes subtle differences in forewing pattern, and on one or more corroborative differences in structure or larval host. Seventeen characters were examined, and study material consisted of more than 1200 pinned adults, 450 genital preparations, and 500 wing preparations. Thirteen species occur only east of the Great Plains, three only westward, and one transcontinentally. Identities are revised for *P. cressoniana* (Clemens), the type species; also for *P. faracana* (Kearfott) and *P. spoliana* (Clemens). *Pseudexentera caryana* McDunnough proved to be a junior synonym of *P. cressoniana*. New species and their type localities are *P. sepia* (Cincinnati, Ohio), *P. hodsoni* (Oak Station, Pa.), *P. knudsoni* (Riviera Beach, Tex.), *P. oreios* (Rustler Park, Ariz.), and *P. vaccinii* (S. March, Ont.). Lectotypes are designated for *P. bipustulana* (Walker) (a junior synonym of *P. costomaculana* (Clemens)), and for *P. oregonana* (Walsingham).

Pseudexentera is a nearctic genus of the tribe Eucosmini. The known larvae appear to be monophagous or stenophagous on woody plant foliage. The adults are among the earliest spring-flying insects. Life history data and adult capture records suggest that all species of *Pseudexentera* are univoltine. At least three species are of economic interest: *P. mali* is a pest of apple, and *P. spoliana* and *P. oregonana* reach conspicuous numbers on oak and aspen, respectively.

Grote (1877) proposed the new genus and species *Exentera aprilana*, and Heinrich (1923) characterized the genus by male genital and other characters without having examined the type specimen. When he discovered that *E. aprilana* is a species of *Eucosma*, Heinrich (1940) proposed the name *Pseudexentera* for the genus, designating *Hedya cressoniana* Clemens as type species, and indicating his earlier belief (Heinrich 1923) that *H. cressoniana* was a junior synonym of *Sciaphila improbana* Walker. McDunnough (1959) discovered that *S. improbana* is a species of *Zeiraphera*. He regarded *Hedya cressoniana* as the type species of *Pseudexentera*, but likewise misidentified it. Thus the genus does not now have a correctly identified type species. The case is being referred to the International Commission on Zoological Nomenclature as called for by Art. 70b of the International Code of Zoological Nomenclature (3rd ed.).

There are two main forewing patterns in the genus, excluding the striped form of some *P. faracana* (Fig. 2). The main patterns are exemplified by *P. cressoniana* (Fig. 1) and *P. costomaculana* (Fig. 22). When forewing pattern varies within species, it ranges between distinct and less distinct or diffuse. Although adults can be identified by external appearance once their variation is understood, the species in each

of the two main wing-pattern groups are confusingly similar. This similarity has thwarted taxonomic progress and fostered confusion, especially with two of the earliest named species, *P. cressoniana* and *P. spoliana,* whose types remained incorrectly identified for more than a century.

METHODS

Pinned adults first were segregated by differences in forewing pattern, sometimes subtle ones. The resulting groups were then examined for differences in structure, larval host, adult phenology, and geography. The number of characters totaled 17. Structure refers to wing venation, genitalia, and body size. Either individual or statistical differences in structure were admissible. One distinguishing character state in structure or larval host was deemed sufficient to confirm specific distinction. Such differences are not always explicitly cited in the text except for new species. If differences beyond forewing pattern were not found, the group in question was combined with the next most similar one. Final groupings thought to comprise species were then assigned names based on their similarity to types.

The following structural characters and states or ranges proved useful in sorting and diagnosing the species. **Both sexes:** origin of forewing veins R_4 and R_5: separate (like M_2 and M_3 in fig. 2 of Heinrich 1923), approximate (like Rs and M_1 in fig. 1 of Heinrich), connate (like M_3 and CuA_1 in fig. 1 of Heinrich), stalked (like M_3 and CuA_1 in fig. 2 of Heinrich). **Males:** position of valval constriction: $\frac{1}{2}$, $\frac{3}{5}$, $\frac{3}{4}$ distance between valval base and apex; maximal valval length/maximal cucullus length ratio, the latter distance measured between upper and lower edges: 1.6 to 3.4; position of anal spine on cucullus: near middle, near lower edge; projections from lower edge of cucullus: absent, one small but conspicuous curved spine present, one or more inconspicuous spinelets or bumps present; radius of curvature of lower edge of cucullus: greater or less than cucullus height; apex of aedeagus: unmodified, falcate, snoutlike and thin, snoutlike and thick; length of forewing: 5.0 to 10.0 mm. **Females:** position of ostium bursae: starting $\frac{1}{10}$ to $1\frac{1}{5}$ width of ostium bursae behind front edge of sternum 7; taper of forward end of sterigma: gradual if any, sharp; lightly sclerotized patch on corpus bursae: present, absent; size of signa: equal or subequal, unequal; symmetry of forward and rear halves of papillae anales: subsymmetrical, asymmetrical; length $\times$ width at maxima of one papilla analis: 0.08 to 0.16 mm^2; length of forewing: 5.5 to 10.0 mm.

Genitalia were prepared as described by Clarke (1941). Position of the ostium bursae was estimated by eye at 45$\times$ nominal magnification. Measurements of papillae anales are to the nearest 0.03 mm, and were

made from microprojections. Valval length/cucullus length ratios were also determined from microprojections. Some wing venation preparations were permanent, but most were temporary. The latter were prepared by touching a capillary tube of xylol to a wing in a microscope field illuminated from below. Subsamples for venation study consisted of equal or nearly equal numbers of males and females when 20 or more adults of a species were available. When fewer adults were available, all were used regardless of the sex ratio. Wing length includes tegula and fringe, and was measured without magnification to the nearest 0.5 mm.

The letter n after a number denotes number of specimens underlying a statement. A parenthetical number after a color name refers to a color in Smithe (1975). Colors were estimated in natural light entering a window. Plant names follow Little (1979).

I examined 1234 pinned adults, 479 genitalia preparations, and 544 wing preparations from 20 sources. All nontypes bear the label "Voucher, W. E. Miller, 1986," and those illustrated here are also marked. The sources, with abbreviations used in the text, are: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Philadelphia; BMNH, British Museum (Natural History), London; CNC, Canadian National Collections of Insects, Arachnids and Nematodes, Ottawa; Craig, W. S. Craig, Columbia, Mo.; CU, Cornell University, Ithaca, N.Y.; FMNH, Field Museum of Natural History, Chicago; Heitzman, J. R. Heitzman, Independence, Mo.; INHS, Illinois Natural History Survey, Urbana; Knudson, E. C. Knudson, Bellaire, Tex.; LACM, Natural History Museum of Los Angeles County, Los Angeles; Leuschner, Ronald Leuschner, Manhattan Beach, Cal.; Mather, Bryant Mather, Clinton, Miss.; MSUE, Michigan State University Entomology Museum, East Lansing; NSM, Nova Scotia Museum, Halifax; UCB, University of California, Berkeley; UMMZ, University of Michigan Museum of Zoology, Ann Arbor; UMSP, University of Minnesota, St. Paul; USNM, National Museum of Natural History, Washington, D.C.; UWM, University of Wisconsin, Madison.

Nomenclatural summaries consist mostly of primary works. Check lists are omitted except where they introduced new name combinations. Keys to species are omitted in the belief that matching specimens to diagnoses and illustrations is a suitable user alternative that saves space.

Pseudexentera Heinrich (1940:243)

Exentera (not Grote 1877:227); Heinrich (1923:172).

Diagnosis. The genus has been characterized by Heinrich (1923) and Brown (1982). **Both sexes:** forewing lacking raised scale tufts, termen notched between veins CuA$_1$ and

M_2. **Males:** lacking forewing costal fold; socii densely setose, fused basally, articulating with tegumen on a stem; valval neck partly clothed with dense spinelike setae, a tiny anal spine on cucullus. **Females:** sternum 7 deeply emarginate around ostium bursae; sterigma consisting of lamella postvaginalis; lamella antevaginalis absent; tergum 9 with two to four tiny backwardly projected spinelets, a trait not previously known; anterior apophyses longer than posterior apophyses; ductus bursae partly sclerotized in an elbow shape near middle; corpus bursae with two finlike signa.

The genus appears to be monophyletic, the stemmed socii constituting a shared and perhaps derived character.

Pseudexentera cressoniana (Clemens)
(Figs. 1, 24, 41)

Hedya cressoniana Clemens (1865:514) (lectotype: Virginia, no date, abdomen missing, forewing length 8.5 mm, Type ... 7222, designated by Darlington 1947, wings illustrated by Miller 1973a, in ANSP).
Exentera improbana (not Walker 1863:337); Heinrich (1923:174) (part).
Pseudexentera caryana McDunnough (1940:243) (holotype: female, St. David's, Ont., 14 April 1938, No. 5105, genitalia illustrated by McDunnough 1940, in CNC). NEW SYNONYMY.

Diagnosis. Forewing pattern (Fig. 1) varying little between or within sexes, but females averaging slightly higher in contrast (90n). Forewing veins R_4 and R_5 usually (92%) stalked at origin, sometimes (8%) connate (48n). In males, valva constricted at ⅗ distance between base and apex, valval length/cucullus length ratio (spine included) 2.0 to 2.2, anal spine near lower edge of cucullus, aedeagus has a falcate apex (10n), a small curved spine projects from lower edge of cucullus (40n) (Fig. 24). The last is readily revealed without dissection by brushing away valval scales. In females, ostium bursae begins ⅙ to ½ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases usually (94%) nowhere fused into a sclerotized patch, and signa unequal in size (Fig. 41) (18n). Forewing length of males 8.5 to 10.0 mm (40n), of females 8.0 to 10.0 mm (45n).

Comments. This species was known most recently as *P. caryana* McDunnough. Heinrich (1923) misidentified it, considering it to be a junior synonym of *Sciaphila improbana* Walker, which he also misidentified. When McDunnough (1959) discovered that the latter represented a species of *Zeiraphera*, he perpetuated Heinrich's misidentification of *P. cressoniana*, apparently unaware that Darlington (1947) had designated a lectotype for the species. Although the lectotype lacks an abdomen, its well preserved forewing pattern (Miller 1973a: fig. 10) is diagnostic. The pattern of *P. caryana* matches it well. This species accounts for the fifth of six known misidentifications of Clemens olethreutine types (Miller 1973a, 1973b, 1974, 1979, 1985).

I examined adults from Connecticut, Illinois, Iowa, Michigan, Mississippi, Missouri, New York, Pennsylvania, Texas, Virginia, and Wisconsin (AMNH, ANSP, Craig, Heitzman, Knudson, Mather, MSUE, NSM, UCB, UMMZ, USNM, UWM). The study sample included the *P. cressoniana* lectotype and a *P. caryana* paratype.

Biology. The larval host is *Carya ovata* (Mill.) K. Koch (McDunnough 1940). Adult capture dates range from 25 February to 16 May (90n).

Pseudexentera faracana (Kearfott)
(Figs. 2–4, 25, 42)

Proteopteryx faracana Kearfott (1907:47) (lectotype male: Scranton, Pa., 21 April 1906, A. E. Lister, genit. prep. CH 15 Dec. 1919, designated by Heinrich 1923, forewing length 9.0 mm, in AMNH).
Exentera faracana; Heinrich (1923:177).
Pseudexentera faracana; Powell (1983:36).
Eucosma haracana (not Kearfott 1907:46); Busck (1914:150).

Exentera spoliana (not Clemens 1865:513) (part); Heinrich (1923:175).
Pseudexentera spoliana (not Clemens 1865:513); MacKay (1959:123), Brown (1982:595).

Diagnosis. Forewing pattern of three slightly intergrading kinds, varying greatly between and within sexes, females possibly averaging higher in contrast. Kinds of pattern are striped (Fig. 2) (7n), thick banded (Fig. 3) (8n), and thin banded (Fig. 4) (35n). Forewing veins R_4 and R_5 usually (73%) approximate or connate at origin, sometimes (27%) stalked or separate (52n). In males, valva constricted at ⅗ distance between base and apex, valval length/cucullus length ratio 2.3 to 2.7, anal spine near lower edge of cucullus, radius of curvature of lower edge of cucullus less than cucullus height, lower edge of cucullus may have up to four inconspicuous projections ranging in shape from bumps to spinelets, aedeagus has thin snoutlike apex (Fig. 25) (16n). In females, ostium bursae begins ⅛ to ½ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases fused on one side near ductus bursae into a lightly sclerotized patch, signa unequal in size (Fig. 42) (25n). Forewing length of males 7.5 to 9.0 mm (19n), of females 7.0 to 8.5 mm (31n).

Comments. This species was most recently known partly as *P. spoliana* and partly as *P. faracana*. The former reflects Heinrich's (1923) misidentification of *P. spoliana*, which has a forewing pattern different from the three *P. faracana* patterns. Kearfott (1907) and Heinrich (1923) mused that one species with variable forewing pattern might be involved. Heinrich kept them separate because there were so few typelike examples of *P. faracana* at the time, the lectotype having the striped pattern. The three patterns here might indeed represent more than one species, but the information available now does not permit more than one to be recognized. Larval hosts are unknown for the striped and thick-banded adults. The larva of the thin-banded adult was described by MacKay (1959).

I examined adults from Connecticut, Illinois, Michigan, Mississippi, Missouri, New York, Ohio, Pennsylvania, Virginia, West Virginia, and Wisconsin (AMNH, ANSP, CNC, CU, FMNH, Heitzman, INHS, LACM, Mather, MSUE, UCB, USNM, UWM). The study sample included the *P. faracana* lectotype and a paralectotype, the pinned adult and genit. prep. No. 252 of Brown (1982), and thin-banded adults reared from *Castanea dentata* (Marsh.) Borkh. (Hopk. U. S. 1134) (4n).

Biology. The larva rolls the leaves of *Castanea dentata*, American chestnut, and the pupa overwinters on the ground (Busck 1914, MacKay 1959). There is one generation per year. Adult capture dates range from 25 February to 10 May (45n).

Although American chestnut was nearly exterminated by the blight fungus *Endothia parasitica* (Murr.) Anders. and Anders. early in this century, the host persists as stump sprouts and occasional disfigured trees. These host remnants could explain how ⅓ of the study sample originated since 1950, two adults as recently as 1982. I captured an adult at stump sprouts. Alternate *Castanea* hosts could also be involved.

Pseudexentera sepia Miller, new species
(Figs. 5, 26, 43)

Exentera spoliana (not Clemens 1865:513) (part); Heinrich (1923:175).

Diagnosis and description. Forewing pattern (Fig. 5) varying little between or within sexes, females possibly averaging higher in constrast (22n). Forewing veins R_4 and R_5 usually (81%) approximate or connate at origin, sometimes (19%) separate or stalked (21n). In males, valva constricted at ⅗ distance between base and apex, valval length/cucullus length ratio 2.2 to 2.6, anal spine near lower edge of cucullus, lower edge of cucullus has one or more inconspicuous projections ranging in shape from bumps to spinelets, aedeagus has thin snoutlike apex (Fig. 26) (7n). In females, ostium bursae begins ⅛ to ⅓ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases fused on one side near ductus bursae into a lightly sclerotized patch, signa unequal in size (Fig. 43) (11n). Forewing length of males 7.0 to 8.5 mm (8n), of females 7.0 to 8.5 mm (14n) (holotype 7.5 mm). *Head.* Labial palpus mixed white and brown, second segment subequal in length to eye diameter, apical

segment ⅓ length of second segment; front and crown mixed white and brown. *Thorax.* Mixed white and brown dorsally, shiny white ventrally; front and middle legs mixed white and brown, hind legs paler, tarsi of all legs banded; forewing upper-side dark markings near burnt umber (22) and raw umber (23), underside pale brown; hindwing upper side pale brown, underside paler. *Abdomen.* Mixed white and brown dorsally, paler ventrally. *Male Genitalia.* Vesica with 14 to 29 deciduous cornuti (5n).

Type data. Holotype female: Cincinnati, OHIO, A. F. Braun, 7 April 1906, genit. prep. DH 813813 (AMNH). Nineteen paratypes (AMNH, CNC, LACM, UCB, UMSP, INHS, Mather, Heitzman, USNM): ILLINOIS: Putnam Co., 31 March 1940, M. O. Glenn, ♀ genit. prep. DH 630812 (Fig. 43); MISSISSIPPI: Vicksburg, 19 Feb. 1982, B. Mather, ♀ genit. prep. WEM 510841; MISSOURI: Kansas City, 19 April 1971, J. R. Heitzman, ♀ genit. prep. SMG 905823; same data except ♂ genit. prep. SMG 907824 (this and preceding captured *in copula*); same data except 18 April 1973 (Fig. 5), wing prep. MGP 24, ♀ genit. prep. WEM 107844; same data except 13 April, ♂ genit. prep. SMG 905822 (Fig. 26); Grundy Co., 5 April 1980, J. R. Heitzman, ♂ genit. prep. SMG 1108828; same data except ♀ genit. prep. SMG 1108827; PENNSYLVANIA: New Brighton, 16 March 1903, H. D. Merrick, ♂, *Proteopteryx spoliana* Clem. AB 1920; same data except ♂ genit. prep. CH 3, 30 Jan. 1920, *Exentera spoliana* Clem. var.; same data except 18 March 1903, ♂, *Exentera spoliana* Clem. AB; same data except 30 April 1907, ♀; Pittsburgh, 22 April 1906, H. Engel, ♀ genit. prep. WEM 175854; QUEBEC: Ottawa Co., 1–7 April, ♀ genit. prep. LKM 824761; Old Chelsea, 30 April 1937, T. N. Freeman, ♀ genit. prep. WEM 107843; same data except 25 April 1935, W. J. Brown, wing prep. MGP 20, ♂ genit. prep. Exen 4A; Aylmer, 9 May 1932, G. S. Walley, ♀ genit. prep. Exen 4A, wing prep. MGP 19; WISCONSIN: Milwaukee, 25 April 1915, H. M. Bower, ♀ genit. prep. WEM 175853; Oneida Co., 20 May 1961, H. M. Bower, ♂ genit. prep. PB 221.

Comments. Heinrich (1923) included this species in what is here considered *P. faracana*, sometimes adding "var." to determinations. The new species most resembles thin-banded *P. faracana*. Among departures in forewing pattern, the basal patch is obscure, unlike that of *P. faracana* (Figs. 4, 5). Also, it is a smaller-bodied insect, based on forewing length. Forewing length of females, the more abundant sex in the study sample, averages 7.6 mm (11n) compared to 8.2 mm (19n) in *P. faracana*. The difference, 0.6 mm, is statistically significant ($t = 3.7$, Pα < 0.001). Although this difference represents only 7% of the longer forewing, it denotes a 25% lighter body weight because of the exponential relation between these variables (Miller 1977).

The species name refers to the family of hues marking the forewing.

Biology. The larval host is unknown. Adult capture dates range from 19 February to 20 May (21n).

Pseudexentera hodsoni Miller, new species
(Figs. 6, 27, 44)

Exentera spoliana (not Clemens 1865:513) (part); Heinrich (1923:175).

Diagnosis and description. Forewing pattern (Fig. 6) varying little between or within sexes (36n). Forewing veins R_4 and R_5 usually (97%) approximate or connate at origin, sometimes (3%) separate (34n). In males, valva constricted at ¾ distance between base and apex, valval length/cucullus length ratio 2.7 to 3.4, anal spine near lower edge of cucullus, radius of curvature of lower edge of cucullus exceeds cucullus height, lower edge of cucullus may have up to two inconspicuous projections ranging in shape from bumps to spinelets, and aedeagus has thin snoutlike apex (Fig. 27) (13n). In females, ostium bursae begins ⅛ to ⅓ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases fused on one side near ductus bursae into a lightly sclerotized patch, signa unequal or subequal in size (Fig. 44) (13n). Forewing length of males 7.0 to 8.5 mm (19n) (holotype 8.0 mm), of females 7.5 to 9.0 mm (17n). *Head.* As described for *P. sepia*. *Thorax.* As described for *P. sepia* except forewing upper-side dark markings near dusky brown (19), and hindwing upper

side grayish brown. *Abdomen*. As described for *P. sepia*. *Male Genitalia*. Vesica containing 22 to 34 deciduous cornuti (4n).

Type data. Holotype male: Oak Station, Allegheny Co., PENNSYLVANIA, 10 April 1910, F. Marloff, genit. prep. CH 20, 13 Feb. 1920, *Exentera spoliana* Clem. det. C. H. (USNM). Thirty-five paratypes (AMNH, Craig, CU, Heitzman, INHS, Knudson, Mather, USNM, UCB): FLORIDA: Pensacola, 7 Feb. 1962, S. Hills, ♂ genit. prep. JAP 1424; ILLINOIS: Putnam Co., 7 April 1963, M. O. Glenn, ♂; same data except 13 April 1941, ♂ genit. prep. WEM 168851; LOUISIANA: Baton Rouge, 14 Feb. 1970, G. Strickland, ♀; MISSISSIPPI: Miss. State Univ., 1 March 1976, C. T. Bryson, ♂ genit. prep. SMG 916822; same data except 19 March, ♀ genit. prep. SMG 1029821 (Fig. 44); Hinds Co., 31 Jan. 1967, B. Mather, ♂ genit. prep. JAP 2441; same data except 13 Feb. 1959, ♂; same data; same data except ♂ genit. prep. SMG 916823; same data except 10 March 1963, ♂ genit. prep. JAP 1578; same data except 16 March 1963, ♀ genit. prep. JAP 1719; Rankin Co., 3 April 1960, B. Mather, ♀ genit. prep. JCL 1107836; Bovina, Warren Co., 7 March 1975, B. Mather, ♀ genit. prep. SMG 915824; same data except ♀ genit. prep. SMG 916821; same data except 14 March 1972, ♀ genit. prep. JCL 1128831; Vicksburg, Warren Co., 4 March 1980, B. Mather, ♀; same data except ♂; same data except 13 March 1981; same data except 30 March 1979, ♀ genit. prep. WEM 207841; Gulfport, 31 March 1978, R. Kergosien, ♀ genit. prep. SMG 916834; MISSOURI: "C. Mo.," reared from red oak, C. V. Riley, ♂ genit. prep. LKM 824765, *Proteopteryx spoliana* Clem. det. Walsingham 1887; Jackson Co., 13 April 1972, J. R. Heitzman, ♂ genit. prep. WEM 207844; same data except 18 April 1979, ♂ genit. prep. WEM 241852; Benton Co., 17 April 1970, J. R. Heitzman, ♂; St. Genevieve Co., 10 April 1981, J. R. Heitzman, ♀ genit. prep. WEM 304851; Columbia, 10 April 1971, W. S. Craig, ♀ genit. prep. JCL 1118833 (Fig. 6); same data except 12 April 1972, ♀ genit. prep. JCL 1118834; same data except 16 April 1971, ♀; same data except 18 April, ♂ genit. prep. WEM 207843; same data except 24 April, ♀; Kirkwood, reared from "L. oak," 1908, Murtfeldt, ♀ genit. prep. WEM 197844; PENNSYLVANIA: Allegheny Co., 30 April 1911, F. Marloff, ♀ genit. prep. JCL 11178310; TEXAS: Anderson Co., 15 March 1983, E. C. Knudson, ♂ genit. prep. ECK 584; Harris Co., 5 Feb. 1984, E. C. Knudson, ♂ genit. prep. ECK 817 (Fig. 27); same data except 19 Feb. 1985, ♂.

Comments. Heinrich (1923) included this species in what is here considered *Pseudexentera faracana*. The new species superficially resembles thin-banded *P. faracana* but differs structurally. The male valval constriction is at ¾ the distance between valval base and apex, compared to ⅗ in *P. faracana*; and the lower edge of the male cucullus is slightly rounded, its curvature forming a circle whose radius exceeds cucullus height, while the lower edge of the cucullus in *P. faracana* is greatly rounded, its curvature forming a circle whose radius does not exceed cucullus height (Figs. 25, 27).

The species is named for Alexander C. Hodson, distinguished entomologist, teacher, and administrator.

Biology. The larval host is *Quercus* (2n), the species being given on labels as "L. oak" and "red oak." According to Riley's label information, the larva "slightly folds . . . leaves in May, pupates in (a) tough cocoon on (the) ground, and emerges early the following spring." Adult capture dates range from 31 January to 30 April (34n).

Pseudexentera knudsoni Miller, new species
(Figs. 7, 28, 45)

Diagnosis and description. Forewing pattern (Fig. 7) varying little within or between sexes (8n). Forewing veins R_4 and R_5 connate, approximate, or stalked at origin (8n). In males, valva constricted at ⅗ distance between base and apex, valval length/cucullus length ratio 2.4 to 2.7, anal spine near lower edge of cucullus, lower edge of cucullus may have up to two inconspicuous projections ranging in shape from bumps to spinelets, aedeagus has falcate apex (Fig. 28) (5n). In females, ostium bursae begins ½ its width

behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases fused on one side near ductus bursae into a lightly sclerotized patch, and signa unequal in size (Fig. 45) (2n). Forewing length of males 6.5 to 7.5 mm (6n) (holotype 7.0 mm), of females 7.0 to 7.5 mm (2n). *Head.* As described for *P. sepia.* *Thorax.* Mixed white, brown, and sometimes orange dorsally, shiny white ventrally; front and middle legs mixed white and brown, hind legs paler, tarsi of all legs banded; forewing upper-side dark markings near olive-brown (28) and glaucous (79); hindwing upper side pale brown, underside paler. *Abdomen.* As described for *P. sepia. Male Genitalia*: Vesica containing 19 to 29 deciduous cornuti (5n).

Type data. Holotype male (Fig. 7): Riviera Beach, Kleberg Co., TEXAS, 24 Feb. 1984, E. C. Knudson, genit. prep. WEM 168855 (USNM). Seven paratypes (Knudson, USNM, UMSP): TEXAS: San Antonio, 2 April 1978, ♂; same data except 6 May, ♂ genit. prep. WEM 154852; Canyon Lake, Comal Co., 8 May 1982, ♂ genit. prep. ECK 325 (Fig. 28); Conroe, Montgomery Co., 9 March 1982, ♂ genit. prep. ECK 570; Benbrook, Tarrant Co., ♂ genit. prep. WEM 168856; Austin, 13 April 1979, ♀ genit. prep. WEM 15852; Sam Houston Nat. For., San Jacinto Co., 29 March 1978, ♀ genit. prep. WEM 35852 (Fig. 45); all E. C. Knudson.

Comments. This species most resembles thin-banded *P. faracana.* Its aedeagus has a falcate apex, whereas that of *P. faracana* has a thin snoutlike apex (Figs. 25, 28). Also, it is a smaller-bodied insect, based on forewing length. Forewing length of males, the more abundant sex in the study sample, averages 6.9 mm (6n) compared to 8.4 mm (18n) in *P. faracana.* The 1.5 mm difference is statistically significant ($t = 7.2$, Pα < 0.001). Although this difference represents only 18% of the larger *P. faracana* forewing length, it denotes a 50% body weight difference because of the exponential relation between these variables (Miller 1977).

The species is named for Edward C. Knudson, its discoverer.

Biology. The larval host is unknown. Adult capture dates range from 24 February to 8 May (8n).

Pseudexentera haracana (Kearfott)
(Figs. 8, 29, 46)

Proteopteryx haracana Kearfott (1907:46) (lectotype female: Hunter's Range, Pike Co., Pa., 1 May 1906, selected by C. Heinrich, designated by Klots 1942, forewing length 6.5 mm, in AMNH).
Exentera haracana; Heinrich (1923:176).
Pseudexentera haracana; Powell (1983:36).

Diagnosis. Forewing pattern (Fig. 8) varying little between or within sexes (67n). Forewing veins R_4 and R_5 usually (82%) connate or approximate at origin, sometimes (18%) stalked or separate (33n). In males, valva constricted at ⅗ distance between base and apex, valval length/cucullus length ratio 2.3 to 2.7, anal spine near lower edge of cucullus, lower edge of cucullus has up to four inconspicuous projections ranging in shape from bumps to spinelets, and aedeagus has thick snoutlike apex (Fig. 29) (14n). In females, ostium bursae begins ⅒ to ⅕ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases fused on one side near ductus bursae into a lightly sclerotized patch, signa unequal in size (Fig. 46) (16n). Forewing length of males 6.0 to 8.5 mm (32n), of females 6.0 to 8.0 mm (35n).

Comments. I examined adults from Connecticut, Florida, Michigan, Minnesota, Mississippi, Missouri, New Jersey, New York, Nova Scotia, Pennsylvania, Texas, and Wisconsin (AMNH, ANSP, Craig, Heitzman, Knudson, LACM, Mather, MSUE, NSM, UCB, UMSP, UWM). The study sample included paralectotypes (2n) and the lectotype. Adults superficially resemble *Gretchena delicatana* Heinrich; the two species are often mixed in collections.

Biology. The larval host is unknown. Adult capture dates range from 26 February to 15 June (67n).

Pseudexentera oreios Miller, new species
(Figs. 9, 30, 47)

Diagnosis and description. Forewing pattern (Fig. 9) varying little between or within sexes (7n). Forewing veins R_4 and R_5 approximate at origin (7n). In males, valva constricted at ¾ distance between base and apex, valval length/cucullus length ratio 2.8 to 2.9, anal spine near lower edge of cucullus, lower edge of cucullus may have one or more inconspicuous projections ranging in shape from bumps to spinelets, aedeagus has thin snoutlike apex (Fig. 30) (4n). In females, ostium bursae begins ¹⁄₁₀ to ⅛ its width behind front edge of sternum, forward end of sterigma tapers gradually, corpus bursae spicule bases fused on one side near ductus bursae into a lightly sclerotized patch, signa subequal in size (Fig. 47) (3n). Forewing length of males 7.5 to 8.0 mm (4n) (holotype 8.0 mm), of females 7.0 to 8.0 mm (3n). *Head.* As described for *P. sepia* except for white front and orange crown. *Thorax.* Similar to crown hues dorsally, shiny white ventrally; legs as described for *P. sepia*; forewing upper-side dark markings near tawny (38) and raw umber (223), the white and silver ocellus conspicuous, underside brown; hindwing upper- and undersides brown. *Abdomen.* Brownish white dorsally, paler ventrally. *Male Genitalia.* Vesica with 25 to 32 deciduous cornuti (3n).

Type data. Holotype male (Fig. 9): Rustler Park, Chiricahua Mts., ARIZONA, 3 July 1972, 8500′ (2600 m), J. Powell, genit. prep. WEM 304853 (UCB). Six paratypes (UCB, UMSP): ARIZONA: Madera Canyon, Santa Rita Mts., Santa Cruz Co., 1–3 Aug. 1970, P. Rude, ♂ genit. prep. WEM 65853; same data except ♂ genit. prep. WEM 307851 (Fig. 30); same data except ♂ genit. prep. JAP 3614; same data except ♀ genit. prep. WEM 307853; Parker Canyon Lk., Cochise Co., 19 July 1972, J. Powell, ♀ genit. prep. WEM 35853 (Fig. 47); same data except ♀ genit. prep. WEM 307854.

Comments. This species most resembles *P. haracana* but differs structurally. The male valval constriction is at ¾ the distance between valval base and apex, compared to ⅗ in *P. haracana*; and the snoutlike aedeagal apex is thin compared to that in *P. haracana*. The species name denotes mountain dwelling.

Biology. The larval host is unknown. Adult capture dates range from 3 July to 3 August (7n).

Pseudexentera spoliana (Clemens)
(Figs. 10, 11, 31, 48)

Hedya spoliana Clemens (1865:513) (lectotype female: Virginia, no date, designated and illustrated by Miller 1973a, forewing length 8.0 mm, only right wings remaining, in ANSP).
Exentera improbana (not Walker 1863:337); Heinrich (1923:174).
Pseudexentera improbana (not Walker 1863:337); Heinrich (1940:242) (part), Mc-Dunnough (1940:244), Freeman (1942:213).
Pseudexentera cressoniana (not Clemens 1865:514); McDunnough (1959:2).
Pseudexentera spoliana; Miller (1973a:223).

Diagnosis. Forewing pattern varying within sexes, overlapping between sexes, females averaging higher in constrast (Figs. 10, 11) (409n). Forewing veins R_4 and R_5 usually (83%) connate or stalked at origin, sometimes (17%) approximate (52n). In males, valva constricted approximately at middle, valval length/cucullus length ratio 1.8 to 2.1, anal spine near lower edge of cucullus, lower edge of cucullus lacks projections, aedeagus has falcate apex (Fig. 31) (44n). In females, ostium bursae begins ⅛ to 1⅖ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases usually (98%) nowhere fused into a sclerotized patch, signa subequal in size (Fig. 48) (62n). Forewing length of males 7.0 to 9.5 mm (194n), of females 6.5 to 9.0 mm (217n).

Comments. The nomenclatural history of this species intertwines with that of *P. cres-*

soniana. Pseudexentera spoliana was long known as *P. improbana,* and most recently as *P. cressoniana* (McDunnough 1959). Because the syntype status of an earlier lectotype (Darlington 1947) seemed doubtful, a more plausible lectotype was designated (Miller 1973a). This action was not destabilizing because the specimens involved are conspecific. Although the lectotype lacks an abdomen, its well preserved forewing pattern (Miller 1973a: fig. 45) is diagnostic. This species accounts for the last of six known misidentifications of Clemens olethreutine types (Miller 1973a, 1973b, 1974, 1979, 1985, and earlier in this paper).

I examined adults from Colorado, Connecticut, District of Columbia, Illinois, Indiana, Iowa, Louisiana, Massachusetts, Michigan, Mississippi, Missouri, New Brunswick, New Hampshire, New Jersey, New York, Nova Scotia, Ohio, Ontario, Pennsylvania, Quebec, Texas, Virginia, and Wisconsin (AMNH, ANSP, CNC, Craig, CU, FMNH, Heitzman, INHS, Knudson, LACM, Mather, MSUE, NSM, UCB, UMMZ, UMSP, UWM). The study sample included the lectotype, adults whose wings were illustrated by Freeman (1942) (3n), and adults reared from *Quercus rubra* L. (24n) and *Q.* sp. (17n). The larva was described by MacKay (1959:122).

Biology. The larva feeds on *Quercus rubra* and perhaps other oaks, rolling the leaves. There is one generation per year (Heinrich 1923, Freeman 1942). Adult capture dates range from 11 February to 30 May (363n).

Pseudexentera mali Freeman
(Figs. 12, 13, 32, 49)

Pseudexentera mali Freeman (1942:213) (holotype male: Bell's Corners, Ont., reared from *Malus sylvestris* (L.) Mill., 7 Feb. 1942, J. McDunnough, wings illustrated by Freeman 1942, No. 5384 in CNC), Chapman & Lienk (1971:52).

Diagnosis. Forewing pattern varying within sexes, overlapping between sexes, females averaging higher in contrast (Figs. 12, 13) (73n). Forewing veins R_4 and R_5 usually (83%) stalked or connate at origin, sometimes (17%) approximate (41n). In males, valva constricted approximately at middle, valval length/cucullus length ratio 1.7 to 1.9, anal spine near lower edge of cucullus, lower edge of cucullus lacks projections, aedeagus has falcate apex (Fig. 32) (11n). In females, ostium bursae begins ¾ to 1⅓ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases nowhere fused into a sclerotized patch, signa unequal or subequal in size (Fig. 49) (16n). Forewing length of males 6.5 to 8.0 mm (33n), of females 6.0 to 7.5 mm (39n).

Comments. I examined specimens from Michigan, Missouri, New York, Nova Scotia, Ontario, Quebec, and Wisconsin (Craig, CNC, CU, Heitzman, MSUE, NSM, UCB, USNM, UWM). The study sample included paratypes (3n), holotype, and adults reared from *Malus sylvestris* (14n).

Biology. The larva feeds on *Malus* spp., mining buds and folding leaves. There is one generation per year, and the pupa winters on the ground (Chapman & Lienk 1971). Adult capture dates range from 13 March to 6 June (58n). The species is considered a pest of apple.

Pseudexentera oregonana (Walsingham)
(Figs. 14, 15, 33, 50)

Semasia oregonana Walsingham (1879:62) (lectotype male: "Camp Watson, Grant Co., Ore., March–April 1872 . . . Type . . . ," genit. prep. No. 5724, selected by N. S. Obraztsov, designated here, forewing length 9.0 mm, in BMNH).
Exentera improbana oregonana; Heinrich (1923:175).
Pseudexentera oregonana; McDunnough (1940:244), Freeman (1942:213), MacKay (1959: 122, 1962:640, 1965:668).
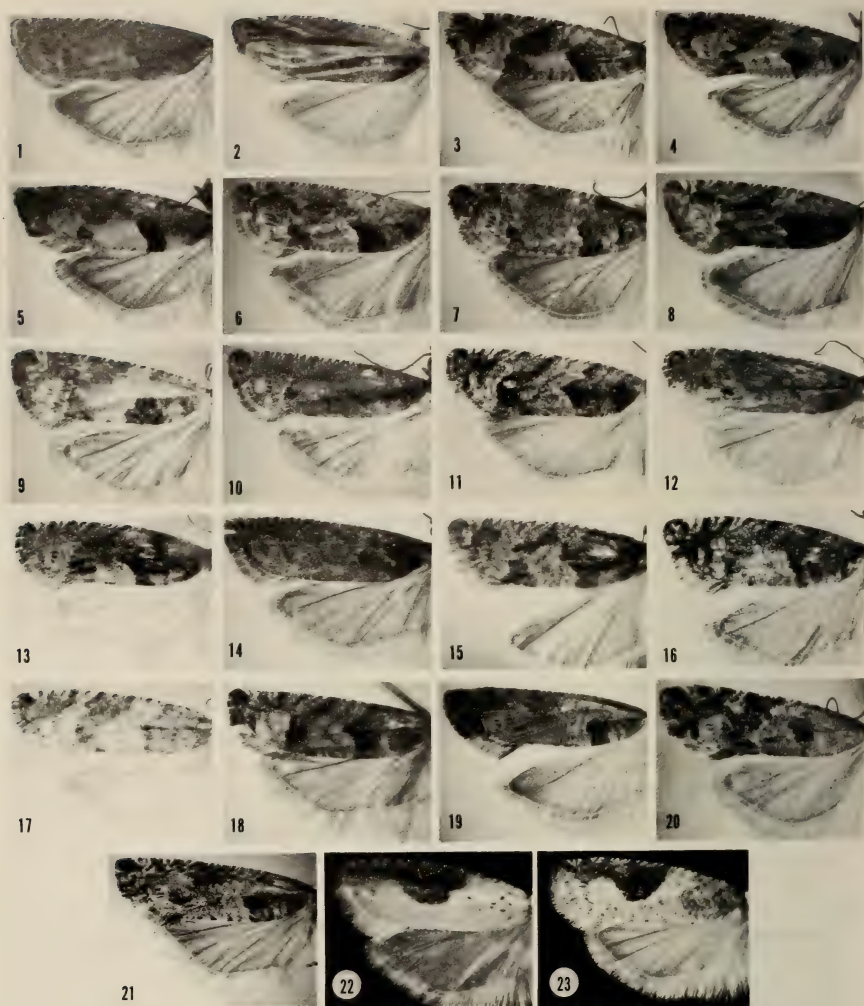
FIGS. 1–23.   *Pseudexentera* wings, some images reversed. (1) *cressoniana* ♂, Columbia, Mo.; (2) *faracana* ♂, Putnam Co., Ill., striped; (3) *faracana* ♀, New Brighton, Pa., thick banded; (4) *faracana* ♀, Falls Church, Va., thin banded; (5) *sepia* ♀, Kansas City, Mo.; (6) *hodsoni* ♀, Columbia, Mo.; (7) *knudsoni* holotype ♂; (8) *haracana* ♀, New Lisbon, N. J.; (9) *oreios* holotype ♂; (10) *spoliana* ♂, Independence, Mo., diffuse pattern; (11) *spoliana* ♀, Aylmer, Que., distinct pattern; (12) *mali* ♂ paratype, Bell's Corners, Ont., diffuse pattern; (13) *mali* ♀ paratype, Bell's Corners, Ont., distinct pattern; (14) *oregonana* ♂, S. Ottawa, Ont., diffuse pattern; (15) *oregonana* ♀, Aweme, Man., distinct pattern; (16) *kalmiana* ♂ paratype, Halifax, N.S.; (17) *maracana* ♂, Shiawassee Co., Mich.; (18) *vaccinii* holotype ♀; (19) *habrosana* ♂, San Luis Obispo Co., Calif., diffuse pattern; (20) *habrosana* ♀, O'Brien, Calif., distinct pattern; (21) *senatrix* ♀ paratype, Cochise Co., Ariz.; (22) *costomaculana* ♀, Dryden, N.Y.; (23) *virginiana* ♂, Ithaca, N.Y.

FIGS. 24–40. *Pseudexentera* male genitalia, some images reversed. (24) *cressoniana*, Livingston Co., Mich., prep. MAM 314792; (25) *faracana*, Mt. Airy, Pa., prep. WEM 137844; (26) *sepia*, Kansas City, Mo., prep. SMG 905822; (27) *hodsoni*, Bellaire, Tex., prep. ECK 817; (28) *knudsoni*, Comal Co., Tex., prep. ECK 325; (29) *haracana*, Lakehurst, N.J., prep. WEM 197843; (30) *oreios*, Sta. Cruz Co., Ariz., prep. WEM 307851; (31) *spoliana*, Blain, Pa., prep. VA 265; (32) *mali*, Oneida Co., Wis., prep. VA 106; (33) *oregonana*, Meach Lk., Que., prep. WEM 97851; (34) *kalmiana*, Mer Bleue, Ont., prep. WEM 135853; (35) *maracana*, Livingston Co., Mich., prep. JAB 80; (36) *vaccinii*, Ingham Co., Mich., prep. JAB 79; (37) *habrosana*, Alameda Co., Calif., prep. WEM 257852; (38) *senatrix* paratype, Cochise Co., Ariz., prep. WEM 237844; (39) *costomaculana*, Ithaca, N.Y., prep. WEM 251852; (40) *virginiana*, Ithaca, N.Y., prep. WEM 251854.

Diagnosis. Forewing pattern varying within sexes, overlapping between sexes, females averaging higher in contrast (Figs. 14, 15) (157n). Forewing veins R_4 and R_5 usually (92%) stalked or connate at origin, sometimes (8%) approximate (37n). In males, valva constricted approximately at middle, valval length/cucullus length ratio 1.9 to 2.2, anal spine near lower edge of cucullus, lower edge of cucullus lacks projections, aedeagus has falcate apex (Fig. 33) (14n). In females, ostium bursae begins ⅕ to 1½ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases nowhere fused into a sclerotized patch, signa unequal or subequal in size (Fig. 50) (18n). Forewing length of males 7.5 to 10.0 mm (85n), of females 7.5 to 9.5 mm (53n).

Comments. I examined adults from Alberta, British Columbia, Maine, Manitoba, Michigan, Nova Scotia, Ontario, Oregon, Quebec, Saskatchewan, and Wisconsin (BMNH,

FIGS. 41–57. *Pseudexentera* female genitalia. (41) *cressoniana*, Barry Co., Mo., prep. SMG 1109824; (42) *faracana*, Putnam Co., Ill., prep. DH 617812; (43) *sepia*, Putnam Co., Ill., prep. DH 630812; (44) *hodsoni*, Oktibbeha Co., Miss., prep. SMG 1029821; (45) *knudsoni*, San Jacinto Co., Tex., prep. WEM 35852; (46) *haracana*, Vicksburg, Miss., prep. SMG 923821; (47) *oreios*, Cochise Co., Ariz., prep. WEM 35853; (48) *spoliana*, Columbia, Mo., prep. SMG 1206821; (49) *mali*, Ithaca, N.Y., prep. WEM 304852; (50) *oregonana*, Ottawa E., Ont., prep. WEM 95854; (51) *kalmiana*, Constance Bay, Ont., prep. WEM 218851; (52) *maracana*, Putnam Co., Ill., prep. DH 701814; (53) *vaccinii*, Washtenaw Co., Mich., prep. VA 252; (54) *habrosana*, O'Brien, Calif., prep. WEM 105853; (55) *senatrix*, Yavapai Co., Ariz., prep. WEM 119851; (56) *costomaculana*, New Brighton, Pa., prep. WEM 301853; (57) *virginiana*, Pittsburgh, Pa., prep. WEM 116852.

CNC, LACM, MSUE, NSM, UCB, UMMZ). The study sample included the lectotype, a paralectotype, adults whose wings were illustrated by Freeman (1942) (3n), and adults reared from *Populus tremuloides* Michx. (23n) and *Salix* sp. (15n).

Biology. The larva eats new foliage and rolls leaves of *Populus tremuloides* and *Salix* sp. There is one generation per year, with the pupa wintering on the ground (Freeman 1942, MacKay 1962, McDunnough 1940, Prentice 1966, Wong & Melvin 1967). Adult capture dates range from 15 March to 14 June (96n).

Pseudexentera kalmiana McDunnough
(Figs. 16, 34, 51)

Pseudexentera kalmiana McDunnough (1959:4) (holotype male: White Point Beach, Queens Co., Nova Scotia, reared from *Kalmia* sp. [*angustifolia* L. according to Ferguson 1975] 15 April 1954, J. McDunnough, genit. prep. WEM 148851, forewing length 6.0 mm, No. 6807 in CNC).

Diagnosis. Forewing pattern (Fig. 16) varying little between or within sexes (58n). Forewing veins R_4 and R_5 usually (80%) connate or approximate at origin, sometimes (20%) stalked or separate (34n). In males, valva constricted at middle, valval length/ cucullus length ratio 1.8 to 1.9, anal spine near lower edge of cucullus, lower edge of cucullus lacks projections, aedeagus has falcate apex (Fig. 34) (14n). In females, ostium bursae begins ⅕ to 1⅖ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases nowhere fused into a sclerotized patch, signa subequal in size (Fig. 51) (16n). Forewing length of males 5.0 to 6.5 mm (36n), of females 5.5 to 6.5 mm (22n).

Comments. I examined adults from Michigan, Newfoundland, New York, Nova Scotia, and Ontario (CNC, CU, MSUE, NMS). The study sample included paratypes (4n) and holotype.

Biology. The larva feeds on *Kalmia angustifolia* L. (Ferguson 1975). Adult capture dates range from 11 April to 14 June (57n).

Pseudexentera maracana (Kearfott)
(Figs. 17, 35, 52)

Proteopteryx maracana Kearfott (1907:46) (lectotype male: Cincinnati, Ohio, 3 April 1906, A. F. Baun, selected by C. Heinrich, designated by Klots 1942, in AMNH).
Exentera maracana; Heinrich (1923:177).
Pseudexentera maracana; Powell (1983:36).

Diagnosis. Forewing pattern (Fig. 17) varying little between or within sexes, females possibly averaging higher in contrast (24n). Forewing veins R_4 and R_5 usually (95%) stalked or connate at origin, sometimes (5%) approximate (22n). In males, valva constricted approximately at middle, valval length/cucullus length ratio 1.6 to 1.8, anal spine near lower edge of cucullus, lower edge of cucullus lacks projections, aedeagus has falcate apex (Fig. 35) (9n). In females, ostium bursae begins ½ to 1½ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases nowhere fused into a sclerotized patch, signa unequal or subequal in size (Fig. 52) (11n). Forewing length of males 7.0 to 7.5 mm (12n), of females 6.0 to 7.0 mm (12n).

Comments. I examined specimens from Illinois, Michigan, Minnesota, Mississippi, Missouri, New York, Ohio, Pennsylvania, Quebec, and Texas (AMNH, CNC, Craig, CU, Heitzman, INHS, Knudson, LACM, Mather, MSUE, UCB, UMMZ). The study sample included the lectotype, a paralectotype, and adults reared from *Crataegus* sp. (4n).

Biology. The larva feeds on *Crataegus*. Adult capture dates range from 30 January to 15 May (20n).

Pseudexentera vaccinii Miller, new species
(Figs. 18, 36, 53)

Diagnosis and description. Forewing pattern (Fig. 18) varying little between or within sexes, females possibly averaging higher in contrast (36n). Forewing veins R_4 and R_5 usually (60%) connate at origin, sometimes (40%) approximate or stalked (30n). In males, valva constricted approximately at middle, valval length/cucullus length ratio 1.8 to 2.0, anal spine near lower edge of cucullus, lower edge of cucullus lacks projections, aedeagus has falcate apex (Fig. 36) (19n). In females, ostium bursae begins ¼ to 1⅛ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases nowhere fused into a sclerotized patch, signa subequal in size (Fig. 53) (16n). Forewing length of males 6.5 to 8.0 mm (21n), of females 6.0 to 7.5 mm (17n) (holotype 7.0 mm). *Head.* Labial palpus brownish white, paler on inner side, second segment subequal in length to eye diameter, apical segment ⅓ length of second; front and crown brownish white. *Thorax.* Hues similar to front and crown dorsally, shiny white ventrally; front and middle legs mixed white and brown, hind legs paler, tarsi of all legs banded; forewing upper-side dark markings near tawny (38) and fuscous (21), underside pale brown; hindwing upper side pale brown, underside paler. *Abdomen.* Brownish white dorsally, paler ventrally. *Male Genitalia.* Vesica with 17 to 23 deciduous cornuti (11n).

Type data. Holotype female (Fig. 18): S. March, ONTARIO, 22 April 1944, J. Mc-Dunnough, reared from *Vaccinium* sp., genit. prep. Exen 11a (CNC). Thirty-seven paratypes (ANSP, CNC, LACM, MSUE, NSM, UMMZ, UMSP): MASSACHUSETTS: Barnstable, 22 June 1951, C. P. Kimball, ♀ genit. prep. *Pseud.* B; same data except 8 July 1950, ♂ genit. prep. *Pseud.* B; MICHIGAN: Ingham Co., 8 April 1967, J. P. Donahue, ♂ genit. prep. JAB 76; same data except ♂ genit. prep. 71; same data except 12 April 1968, ♂; same data except ♀ genit. prep. WEM 87853; same data except ♀ genit. prep. JAB 69; same data except ♂ genit. prep. VA 277; same data except ♂ genit. prep. VA 278; same data except ♂ genit. prep. VA 279; same data except 15 April 1967, ♂ genit. prep. JAB 79 (Fig. 36); same data except 26 April 1970, ♀ genit. prep. HS 3177311; same data except 2 May 1968, ♀ genit. prep. WEM 87851; same data except 18 May 1966, ♀ genit. prep. PJ 61; Chippewa Co., 25 May 1966, J. P. Donahue, ♀ genit. prep. PJ 54; same data except ♂ genit. prep. PJ 56; Otsego Co., 3 May 1970, J. P. Donahue, ♂ genit. prep. HS 317787; Crawford Co., 28 April 1951, R. R. Dreisbach, ♂ genit. prep. RBM 198; Washtenaw Co., 14 April 1936, W. W. Newcomb, ♀ genit. prep. VA 252 (Fig. 53); Midland Co., 21–31 May 1961, R. R. Dreisbach, ♀ genit. prep. PJ 234; MINNESOTA: Cass Co., 14 May 1936, R. H. Daggy, ♀ genit. prep. ACC 427781; NEW JERSEY: New Lisbon, 24 April 1933, E. P. Darlington, ♀ genit. prep. KL 191; same data except 6 May, ♀ genit. prep. WEM 1022735; same data except ♂ genit. prep. WEM 218853; same data except 14 May, ♂ genit. prep. WEM 1022734; same data except 16 May, ♂ genit. prep. KL 196; same data except 14 May 1932, ♂ genit. prep. KL 195; ONTARIO: Same data as holotype except ♀ genit. prep. WEM 85853; Bell's Corners, 20 April 1941, T. N. Freeman, ♀; same data except ♀ genit. prep. LKM 824769; same data except 25 April, ♂ genit. prep. WEM 87855; Constance Bay, 28 April 1941, J. McDunnough, ♂ genit. prep. WEM 218852; same data except T. N. Freeman, ♂; same data except ♂ genit. prep. Exen 11; same data except 26 April 1935, W. J. Brown, ♂ genit. prep. WEM 87854; same data except G. S. Walley, ♂ genit. prep. WEM 177841; PENNSYLVANIA: Allegheny Co., 10 April 1910, F. Marloff, ♀ genit. prep. WEM 97853.

Comments. This species most resembles *Pseudexentera maracana*. It differs in its thinner middle forewing crossband (Figs. 17, 18), its statistically different R_4 and R_5 origins, its statistically different ostium bursae position and in larval host. The frequency distribution of approximate, connate, and stalked R_4 and R_5 origins is 7, 18, and 5, respectively, compared to 1, 10, and 11 in *P. maracana* (G_{adj} = 10.4, $P\alpha$ < 0.01). In *P. vaccinii* the ostium bursae begins on average 0.58 its width behind the front edge of the sternum compared with 0.95 in *P. maracana*. The difference, 0.37, is significant (t = 3.50, $P\alpha$ < 0.01). The unnamed *Pseudexentera* larva on *Vaccinium* described by MacKay (1959:121) is probably this species.

Biology. The larva feeds on *Vaccinium* (2n). Adult capture dates range from 8 April to 8 July (36n).

Pseudexentera habrosana (Heinrich)
(Figs. 19, 20, 37, 54)

Exentera habrosana Heinrich (1923:178) (holotype male: San Diego, Calif., 17 March
    1912, W. S. Wright, genitalia illustrated by Heinrich 1923, No. 24833 in USNM).
Pseudexentera habrosana; Powell (1961:203).

Diagnosis. Forewing pattern varying within sexes, overlapping between sexes, females possibly averaging higher in contrast (Figs. 19, 20) (59n). Forewing veins R_4 and R_5 usually (97%) approximate or connate at origin, sometimes (3%) stalked (56n). In males, valva constricted approximately at middle, valval length/cucullus length ratio 1.8 to 2.1, anal spine located near lower edge of cucullus, lower edge of cucullus may have up to two inconspicuous projections ranging in shape from bumps to spinelets, aedeagus has falcate apex (Fig. 37) (20n). In females, ostium bursae begins ⅔ to 1½ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases nowhere fused into a sclerotized patch, signa subequal or unequal in size, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases nowhere wing length of males 7.5 to 9.5 mm (35n), of females 7.0 to 8.5 mm (24n).

Comments. I examined adults from the California counties of Alameda, Contra Costa, Lake, Los Angeles, Marin, Mendocino, Orange, Placer, Riverside, San Diego, San Francisco, San Luis Obispo, Santa Barbara, Santa Clara, Shasta, Sonoma, Stanislaus, Tuolumne, and Ventura (LACM, Leuschner, UCB, USNM). The study sample included adults listed by Powell (1961) (6n), adults reared later by Powell from *Quercus agrifolia* Née or *Q. wislizeni* A. DC. (12n), and a paratype. The larva was described by Powell (1961).

Biology. The larva feeds on *Q. agrifolia* and *Q. wislizeni* foliage. Adult capture dates range from 21 January to 17 April (47n).

Pseudexentera senatrix (Heinrich)
(Figs. 21, 38, 55)

Exentera senatrix Heinrich (1924:390) (holotype male: Paradise, Cochise Co., Ariz., 8–
    15 March, in USNM).
Pseudexentera senatrix; Powell (1983:36).

Diagnosis. Forewing pattern (Fig. 21) varying little within or between sexes, females possibly averaging higher in contrast (25n). Forewing veins R_4 and R_5 usually (90%) connate or stalked at origin, sometimes (10%) approximate (20n). In males, valva constricted approximately at middle, valval length/cucullus length ratio 2.0 to 2.1, anal spine near lower edge of cucullus, lower edge of cucullus may have up to four inconspicuous projections ranging in shape from bumps to spinelets, aedeagus has falcate apex (Fig. 38) (6n). In females, ostium bursae begins ½ to 1⅙ behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases nowhere fused into a sclerotized patch, signa unequal or subequal in size, forward and rear halves of papillae anales subsymmetrical in outline (Fig. 55) (7n). Forewing length of males 8.0 to 8.5 mm (16n), of females 8.0 to 8.5 mm (9n).

Comments. I examined adults from Arizona and San Bernardino Co. (Barnwell, New York Mts.), California (Leuschner, LACM, UCB, USNM). The study sample included paratypes (3n).

This species has not been adequately differentiated from any congener. It most resembles *P. habrosana*. It differs statistically in R_4 and R_5 origin, in size as well as symmetry of papillae anales, and in other ways. The frequency distribution of approximate, connate, and stalked R_4 and R_5 in *P. senatrix* is 2, 10, and 8, respectively, compared to 33, 21, and 2 in *P. habrosana* (G_{adj} = 22.0, Pα < 0.005). Length × width maxima of one papilla analis ranges from 0.14 to 0.16 mm² in *P. senatrix* (7n) compared to 0.08 to 0.12

mm² in *P. habrosana* (12n). The respective means are 0.15 and 0.10, and the difference, 0.05, is significant with or without dividing individual values by forewing length to adjust for body size ($t \geq 8.4$, $P\alpha < 0.001$). Also, forewing pattern varies less in *P. senatrix* than in *P. habrosana*. The former has coarse-grained ashy gray forewings, with brown scaling in the terminal area obscure and visible only under magnification. The latter has fine-grained forewing coloration with brown scaling conspicuous in the dark areas and often elsewhere as well. The two species are allopatric, *P. senatrix* occurring in Arizona and southeastern California, and *P. habrosana* in many areas of California, but not in the southeastern part. The known larval hosts of *P. habrosana* do not occur in the range of *P. senatrix*, which indicates the latter has a different host or hosts.

Biology. The larval host is unknown. Adult capture dates range from 18 March to 6 May (25n).

Pseudexentera costomaculana (Clemens)
(Figs. 22, 39, 56)

Anchylopera costomaculana Clemens (1860:349) (lectotype female: North America, no date, No. 139, designated by Darlington 1947, forewing length 7.0 mm, wings illustrated by Miller 1973a, in ANSP).

Batodes bipustulana Walker (1863:316) (lectotype female: "N. Amer. . . . , Type . . . ," no date, genit. prep. No. 11635, selected by N. S. Obraztsov, designated here, forewing length 7.5 mm, in BMNH).

Exentera costomaculana; Heinrich (1923:178).

Pseudexentera costomaculana; McDunnough (1954:2), MacKay (1962:640).

Diagnosis. Forewing pattern (Fig. 22) varying little between or within sexes, pale areas near yellow ocher (123C) (60n). Forewing veins R_4 and R_5 approximate or separate at origin (27n). In males, valva constricted at ⅗ distance between base and apex, valval length/cucullus length ratio 2.8 to 2.9, anal spine near middle of cucullus, aedeagus has unmodified apex (Fig. 39) (8n). In females, ostium bursae begins ⅙ to ¼ its width behind front edge of sternum, forward end of sterigma tapers sharply, corpus bursae spicule bases fused on one side near ductus bursae into a lightly sclerotized patch, signa unequal in size (Fig. 56) (8n). Forewing length of males 6.5 to 8.5 mm (19n), of females 7.0 to 8.0 mm (13n).

Comments. I examined adults from Connecticut, Maryland, Michigan, Mississippi, New Hampshire, New York, North Carolina, Nova Scotia, Pennsylvania, and West Virginia (LACM, MSUE, NSM, UCB, UMMZ, USNM). The study sample included adults reared from *Hamamelis* sp. (prob. *virginiana* L.) (3n), and lectotypes of *P. costomaculana* and *P. bipustulana*. The larva was described by MacKay (1962).

Biology. The larva mines buds and folds leaves of *Hamamelis virginiana* L., and the pupa winters (McDunnough 1954, MacKay 1962, Ferguson 1975). Adult capture dates range from 9 April to 18 July (55n).

Pseudexentera virginiana (Clemens)
(Figs. 23, 40, 57)

Anchylopera virginiana Clemens (1865:512) (type unknown).

Exentera virginiana; Heinrich (1923:179).

Pseudexentera virginiana; Miller (1973a:224).

Diagnosis. Forewing pattern (Fig. 23) varying little between or within sexes, pale areas near drab (27) (46n). Forewing veins R_4 and R_5 approximate or separate at origin (22n). In males, valva constricted at ⅗ distance between base and apex, valval length/cucullus length ratio 2.5 to 2.6, anal spine near middle of cucullus, aedeagus has unmodified apex (Fig. 40) (6n). In females, ostium bursae begins ¼ to ⅔ its width behind front edge of sternum, forward end of sterigma tapers sharply, corpus bursae spicule bases fused on

one side near ductus bursae into a lightly sclerotized patch, signa unequal in size (Fig. 57) (8n). Forewing length of males 7.5 to 9.0 mm (9n), of females 7.5 to 9.5 mm (13n).

Comments. I examined adults from Connecticut, Maryland, Michigan, Mississippi, New York, Pennsylvania, and South Carolina (LACM, Mather, MSUE, UCB, UMMZ, USNM).

Biology. The larval host is unknown. Adult capture dates range from 7 March to 11 May (46n).

Conclusion

Only three adults, less than 0.3% of the number studied, were not satisfactorily resolved to any of the above species (UCB, CNC, MSUE). All three are different and may represent extreme variants of named species or single examples of unnamed species.

Of the 13 species previously recognized (Powell 1983), the names of eight appear valid, and the names of five are revised here. With the five new species described here, the number of *Pseudexentera* species now totals 17. Thirteen occur only east of the Great Plains, three occur only westward, and one is transcontinental. The following table of equivalents summarizes *Pseudexentera* species names here relative to those in Hienrich's (1923) revision:

Here	Heinrich
cressoniana (Clem.)	*improbana* (part)
faracana (Kft.)	*faracana* and *spoliana* (part)
sepia n. sp.	*spoliana* (part)
hodsoni n. sp.	*spoliana* (part)
knudsoni n. sp.	—
haracana (Kft.)	*haracana*
oreios n. sp.	—
spoliana (Clem.)	*improbana* (part)
mali Freeman	—
oregonana (Wlsm.)	*improbana oregonana*
kalmiana McD.	—
maracana (Kft.)	*maracana*
vaccinii n. sp.	—
habrosana (Heinr.)	*habrosana*
senatrix (Heinr.)	—
costomaculana (Clem.)	*costomaculana*
virginiana (Clem.)	*virginiana*

So far as known, larval host associations by plant family and number of *Pseudexentera* species are: Fagaceae (4), Rosaceae (2), Ericaceae (2), Juglandaceae (1), Salicaceae (1), and Hamamelidaceae (1). Larval hosts are unknown for six species. Fragmentary larval host information may be the single greatest deficiency hindering progress and strengthening of *Pseudexentera* taxonomy.

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GENERAL NOTE

AN INTER-SUBFAMILIAL MATING INVOLVING AN ENDANGERED
BUTTERFLY (LYCAENIDAE: LYCAENINAE AND RIODININAE)

I report here an inter-subfamilial mating between a female *Euphilotes battoides allyni* (Shields) (Lycaeninae) and a male *Apodemia mormo virgulti* (Behr) (Riodininae). The former is commonly known as the El Segundo blue butterfly, and is recognized as endangered by the U.S. Fish & Wildlife Service.

The mating was observed on 18 July 1984 at a remnant of the El Segundo sand dune system at the western end of the Los Angeles International Airport (LAX), Los Angeles Co., CA. During July and August 1984, I conducted a capture-recapture study of the El Segundo blue at LAX to collect baseline information on the butterfly's ecological requirements and to estimate its population size. My study was sponsored by the California Department of Fish & Game.

The mating pair (Fig. 1) was first noted at 1232 h PDT perched about 4 cm above the ground on foliage of *Erysimum suffrutescens* (Abrams) G. Rossb. (Brassicaceae). The wing condition of both specimens was fresh, suggesting they were no more than a few days old. The crucifer was surrounded by a patch of about 15 *Eriogonum parvifolium*

FIG. 1. The inter-subfamilial mating pair, *Euphilotes battoides allyni* (top) and *Apodemia mormo virgulti* (bottom).

Sm. in Rees. (Polygonaceae), larval and primary adult foodplant of both lycaenids at LAX. These plants were located approximately 75 m E of the airport's main radar installation in the SE portion of the dunes, where they grew just below the ridgetop of a sand hill at about 50 m elevation. Earlier, at 1207 h PDT, I recorded a temperature of 31°C, with bright, sunny skies, and a slight breeze from the W measuring about 8 km/h.

While I tried to photograph the mating pair, it made three short flights, moving no more than about 3 m with each effort. The female *allyni* was the active flyer. The pair first landed on the sandy substrate, then on a dead specimen of *Erysimum suffrutescens*, and finally on a twig of an unidentified dead plant. Copulation ceased at 1337 h PDT, and the female *allyni* immediately flew away, while the male *virgulti* remained motionless for another 4 min before it resumed normal activity.

The female *allyni* was marked while the pair was mating, and it was observed later that day nectaring and ovipositing on *E. parvifolium* in the same area. I collected a single egg and the female to obtain more eggs. During the next 3 days, the female *allyni* laid 22 eggs in confinement before expiring. Upon dissecting the female's abdomen, I found a properly formed spermatophore. The eggs were examined microscopically and compared to fertile *allyni* eggs. All eggs were typical of *allyni*; however, none were viable. I previously reared *allyni* and found that larvae hatch within 4 to 8 days after oviposition (Arnold, 1983, Univ. Calif. Publ. in Entomol. 99:1–161). I dissected all 23 eggs about 3 weeks after they were laid, and found no evidence of developing larvae. Probably a breakdown in a premating, reproductive-isolating mechanism (perhaps behavioral stimuli) led to this unusual mating, but apparently no hybrid offspring were produced due to the action of one or more postmating, reproductive-isolating mechanisms such as gametic mortality, zygotic mortality, or hybrid inviability.

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BOOK REVIEWS

BRITISH PYRALID MOTHS. A GUIDE TO THEIR IDENTIFICATION, by Barry Goater, 175 pp., col. frontispiece, 8 col. pls., 12 text figs. Harley Books, Great Horklesley, Colchester, Essex CO6 4AH, England. Distributed by Apollo Books, Lundbyvej 36, DK-5700 Svendborg, Denmark.

This is an admirable work, a happy combination of excellence and meticulousness by author, illustrators, and publisher who clearly kept the user uppermost in mind. It meets its primary stated purpose, identification, by illustrations and descriptions. It deals with 208 species but there are 264 individual color photographs of the moths, by Geoffrey Senior, supplemented by 58 drawings by Robert Dyke of genitalic and other characteristics of closely related species, and by structural diagrams. The descriptions of the distinguishing features of the species are concise. There are no keys, which anyway are too often inadequate excuses for failures to provide adequate figures, and they are neither needed nor missed.

This book is more than merely a competent and overdue aid to identifications. More than most works of its kind it gives information on the distributions (including Ireland and the Channel Islands), habits, behavior, life histories, foodplants (with a separate index to these), and collecting histories, reflecting the wide natural history interests of its author. Such information is of value in indicating what is not known and thus needs to be found out. The early stages of such common species as *Crambus pascuella* and *Scoparia ambigualis* are still undescribed. Species such as *Scoparia ancipitella* and *Crambus ericella* which have northerly distributions in Great Britain should be found in Ireland. Are the three alpine species that were recorded from the mountains of Scotland or northern England in Victorian times and not since then natives that await rediscovery? Why does *Ostrinia nubilalis* feed exclusively on *Artemisia* in Britain?

In the 35 years since the publication of the previous book on these moths, the number of known British species went from 174 to 208. Eighteen, perhaps 20, of the 34 additions were introduced species, 11 of them on aquatic plants, and most of the remainder on stored food products. About 10 were previously unrecorded migrants or vagrants from continental Europe. Only two, and perhaps a third, were apparently previously overlooked natives. These additions are in part offset by the dozen or so species that were recorded in the 19th century but not since. Some of these may yet be rediscovered: the only British records for *Acigonia cicatricella* are 100 years apart.

Changes in the abundance of individual species during the past 35 years are noteworthy. Increases have been of a few established immigrants and introduced species. Some decreases clearly were from human activities: improvements in farming hygiene that have been detrimental to the barn-inhabiting or hay-feeding *Aglossa* spp. and *Pyralis lienigialis*, in bee-keeping to *Galleria mellonella*, and perhaps in hedge cutting to *Numonia advenella*, which likes old, uncut hawthorns. The decline in the extent of chalk downlands, and the damage by visitors and developers to sandy coastal areas may be primary reasons for decreases in at least five species of those habitats.

Whether or not weather changes have had significant effects is not clear. It may not be coincidence, however, that the 30 or so species that inhabit relatively dry situations, as on sandhills or sandy or chalky soils or limestone pavement, appear as a whole to be more local and less common where they occur than the inhabitants of wet situations; or that the two migrants that became established within the last 35 years, *Phlyctaenia perlucidalis* and *Ancylosis oblitella*, like damp situations, whereas the one species that has not been found since 1960, *Eurhodope cirrigerella* (incidentally, a generic name not in the index) is believed to require hot, dry summers. In any event, the fact that so many species are capable of flying across the English Channel, and much greater distances to Ireland, is one indication of how quickly a long-term weather change could be followed by changes in the lepidopterous fauna of Britain.

The publisher's advertisement on the book-jacket states that Mr. Goater had to be persuaded to write this book. Whoever did the persuading deserves our thanks and congratulations.

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NORDEUROPAS PYRALIDER, DANMARKS DYRELIV. Bind 3, by Eivind Palm. Fauna Bøger, København, Denmark, 287 pp., including 8 color plates, 264 black and white figures, and distribution maps of 219 species, 1986. Distributed (as well as volumes 1 and 2 of the series) by Apollo Books, Lundbyvej 36, DK-5700 Svendborg, Denmark. Price: Danish Kroner 400.00 + postage (15% discount for subscribers to the series).

This useful Danish-language book invites comparison with the almost simultaneously published *British Pyralid Moths,* by Barry Goater. Palm's book deals with a larger fauna—219 species actually recorded from Fennoscandia and immediately adjacent parts of the Netherlands, North Germany and Poland, with brief notes on some 50 more species that might be expected, compared with 209 species, including accidentals and greenhouse pests, on the British list. However, several species on the British list are not represented in the present treatment. On the whole the treatment of species is more extensive in this book than in Goater's; the distributional information is more detailed and is supplemented by dot maps of distribution in the region and more detailed maps of the distribution in Denmark of species that occur there. For anglophone readers there is a "Summary" paragraph for each Danish species, in which geographical distribution in Denmark, habitat, and times and months of flight are briefly stated. Though this courtesy will be appreciated, one wonders why a similar summary was not given for the non-Danish species as well. The numerous black and white figures of genital and other structures and of wing patterns will be useful in distinguishing close species. The color plates are clear, neat, and satisfactory for recognition, but have not achieved the brilliance of those in Goater's book. Palm has picked up some late species synonymy that was missed by Goater, but otherwise the two classifications are extremely close, a fact that will be a blessing for European lepidopterists. *Nordeuropas Pyralider* is convenient in size and attractively produced. It has few blemishes, but there is some typographical confusion on line 2 of the captions for Figs. 205–210.

Language and geography will in large part determine the readership of these two books, but the specialist in Pyralidae and the general student of North European moths ought to have both. As a reference for purchase by libraries, museums and universities, *Nordens Pyralider* can be recommended heartily.

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OBITUARY

Laurence Remington Rupert (1902–1978)

In 1977, we wrote to Laurence R. Rupert to request historical information on the Southern Silvery Blue [*Glaucopsyche lygdamus* (Doubleday)] locality which he had discovered near Horseheads, Chemung County, New York, 30 years before. Over the next several months we had a regular correspondence, in the course of which Mr. Rupert told us much about his life and Lepidoptera collecting experiences. Rupert died soon after, and since he was a charter member of the Lepidopterists' Society and remained a member until his death, we prepared this brief (and certainly incomplete) biography, drawing heavily from his own letters written on the dates indicated at the end of quoted passages. Occasionally we add explanatory insertions in square brackets.

Laurence Remington Rupert was born southeast of Buffalo, at Sardinia, Erie Co., New York, on 2 July 1902. His parents were Clara Remington Rupert and Asahel Rupert. He grew up in this area, and early became interested in Lepidoptera:

> When I was about twelve years old—in 1914—I got the idea that is not rare among boys of that age, that I would like to collect butterflies. I had no sponsor, and had no real idea how to go at the job, but my father bought me a copy of Holland's *Butterfly Book*. I managed to acquire a rather messy collection of about 35 species of butterflies that were more or less common here at the time. But I lost interest when I seemed unable to get any more species, and when the collection I had fell prey to Dermestids.
>
> However, I did get quite well acquainted with those 35 or so species, and was able ever afterward to identify them. I could not get interested in skippers, for I was rarely able to identify them from Holland's plates. . . .
>
> By the early 1920's I was in college in Albany. (I graduated from the then N.Y.S.C.T. in 1924 [now State University of New York at Albany].) I was not collecting butterflies nor moths, but was, as always, interested in hiking over the country (12 July 1977). The sand barrens west of the city [now known as the Albany Pine Bush] were pretty much intact, and there were vast acres solid blue with lupine [*Lupinus perennis*] blossoms. . . . There were occasional plants interspersed with white or pink flowers. . . . I probably saw more blooms of it at once than I ever saw of any other flower (15 June 1977).
>
> Several years later I went back to Albany for some graduate work and I was by that time collecting moths, Geometridae in particular. I became acquainted with Al Frederick at that time and went with him a few times to the area where the lupines grew. But he was interested in daytime collection of butterflies, and I was not collecting butterflies. I do have perhaps half a dozen geometrid moths in my collection that I took there, but nothing really special, only species that I later collected on the acid soil hills at Horseheads. One of those species is *Catopyrrha coloraria*, which tells me that there must be *Ceanothus* growing among the lupines (12 July 1977). [*Ceanothus americanus* is frequent in the Pine Bush.]

In 1933–1934, Rupert attended Cornell University Graduate School in Ithaca, New York, where he studied mathematics. During this time he met W. T. M. Forbes and John G. Franclemont, and in spring 1934 he and Franclemont collected together in the Sixmile Creek gorge near Ithaca. Later that year he journeyed to Mount Washington:

> In the summer of 1934, Al Frederick accompanied me on a collecting trip to Mt. Washington. I got a few nice moths there, and I believe he was quite successful with the butterflies he sought. . . . Later our communications gradually faded out, for we really had little in common (12 July 1977). [Frederick's collection is in the American Museum of Natural History in New York City—Rindge (1967).]

In autumn 1934, Rupert started working at the Horseheads High School in Horseheads, New York, where he taught mathematics until 1950. His collecting of moths continued regularly, but he also discovered a butterfly there that has been rarely encountered in New York, *Glaucopsyche lygdamus*:

At Horseheads I was collecting almost exclusively at night. But now and then, possibly on a Sunday afternoon, I would explore new areas by day, looking for possible new collecting spots, and it was on one of those trips [in 1947] that I stumbled into the area where the *Glaucopsyche* were flitting about. Somehow I thought they looked a little odd, although I wasn't sure. So I took a few and showed them to Dr. Forbes the next time I went to Ithaca. He identified them, said they were a very nice thing. . . . At one time or another I picked up quite a few, for I found there were a few moth collectors with whom I was regularly exchanging, who wanted them. [See Dirig & Cryan, in prep., for details of *Glaucopsyche lygdamus* in New York.] Those are probably the only butterflies that I have collected in over 60 years [except for some on a 1950 trip] . . . in New Brunswick and the Gaspé, which I gave to the Cornell University Collection (12 July 1977). (See Ferguson & Rupert 1951.)

During his years in Horseheads he also discovered *Lambdina canitiara* Rupert. This new geometrid moth was described from four males and a female taken at Horseheads between 1938 and 1943 (Rupert 1944). Rupert described the type locality as follows:

They were all taken along the base of the next hill north of the Latta Brook, east of the southern end of Horseheads Village. I am sure that the entire area is now occupied by Route 17. However, it seems as if there must be other spots among those Southern Tier hills where the species must occur. It did not seem to be an area unique in any special way. The hill was well wooded, but the trees became scatter[ed] at the base, and there was a small swampy area near by, where there were alders [*Alnus* sp.] and cattails [*Typha* sp.]. I used to get *Tacparia detersata* there and *Sthenopis argenteomaculatus*. I do not believe that the swamp area had any connection with the *Lambdinas*. All the known species of that genus have either oak [*Quercus* sp.] or pine [*Pinus* sp.] as the larval food, and most related genera do too. Moreover, I never found the moths in the swamp, but possibly 100 feet east, toward the hill (8 August 1977).

Mr. Rupert was particularly interested in Geometridae, subfamily Ennominae, and published three additional papers on this group: "A Specific Revision of the Genus *Metarranthis*" (1943), "A Revision of the North American Species of the Genus *Plagodis*" (1949a), and "Notes on the Group of Genera Including *Lozogramma* Stephens and its Allies" (1949b). New combinations were made and several new species were described in these papers.

After leaving his teaching position in 1950, Rupert returned to Sardinia, where he grew gladioli commercially for a number of years. He also worked for an electronics company at Arcade, New York, a few miles east of Sardinia. Throughout this time he continued to collect moths, but a heart ailment curtailed his activities somewhat in later years. In summer 1977 he still had half an acre of gladioli, and exhibited at the annual picnic and early seedling show of the Empire State Gladiolus Society in West Elmira on 7 August. At that time we planned to meet, and he described himself as "easily identifiable. I am 75 years old, 5 ft. 4 in. tall and weigh about 110 pounds" (25 July 1977). He was also the organist in the United Methodist Church in Sardinia.

When we asked him about patronyms, he answered

Yes, Franclemont's form *ruperti* of *Catocala cerogama* is named for me. So is the species *Chytonix ruperti* of the Noctuidae, which was described by Jack Franclemont from a series of over 60 specimens that I took at Versailles, N.Y. [west of Sardinia]. These are distributed in museums pretty well over the country. Dr. McDunnough also named a variety of *Zale helata* with the same name *ruperti,* and along with it he named a similar looking variety of *Zale duplicata, franclemonti* (12 July 1977).

Mr. Rupert died on 13 November 1978. His moth collection is now in the Cornell University Insect Collection. Franclemont facilitated its acquisition, and told us that it was housed in ca. 125 Cornell drawers, of which 60 were noctuids. There were no butterflies in it at the time of Rupert's death, these having been given to Cornell via Forbes years before. The Cornell Insect Collection has recently been moved to the new John H. and Anna B. Comstock Hall, within a compacterized arrangement of cases, and is being reorganized. Rupert's specimens are still in units throughout the series, awaiting

incorporation by species. Franclemont has a map of Rupert's favorite collecting areas (J. G. Franclemont, pers. comm., 10 March 1986).

In communications with us, Rupert made some notes on collecting sites, and reflected upon changes in habitats and the moth fauna during his lifetime:

A great number of specimens in my collection are labeled RICHMOND GULF, SARDINIA, N.Y. Richmond Gulf is a deep ravine about seven miles west of the village, but in the Town of Sardinia. It is not more than a quarter of a mile long. Today it is heavily wooded, and I find it very unproductive in recent years. But in the [19]30's and [19]40's it was much more open and produced a lot of fine moths. . . . All specimens labeled EAST CONCORD, N.Y. were taken on a sphagnum bog easily located on a map. Also, those labeled EAST ARCADE, N.Y. were taken on another bog about ten miles northeast of here, *or* were taken on an unusual, dry, acid soil area adjacent to the bog, and I know which are which. For example, on the dry area there are acres of black chokeberry (*Aronia melanocarpa*) which supports a population of *Catocala praeclara*, so far as I know the only . . . colony in the state west of the Hudson valley and Adirondacks. I also have a few other records from there of species that I have never seen elsewhere in western New York.

One odd record that I have is for *Merolonche dolli,* which I took on the ceiling of my classroom in Horseheads. We had had a "Parents' Night" on a hot evening in May, and I had all the windows open. When it was all over I noticed the strange moth on the ceiling. I scared up a stepladder and captured it. So far as I know it is the only record from upstate New York. I also have a specimen of *Callopistria floridensis* taken on the front wall of the YMCA Building in Binghamton, the only New York State record, I believe. This was almost certainly a stray, for it was taken in October when certain strays are common.

There was much of interest in *Atala* [volume 4]. I was definitely interested in two moths mentioned [by Hessel (1976)]. In 1936 I found a female *Sphinx luscitiosa* on a fencepost at Horseheads. It was so battered and worn that it could not be identified except by genus. I put her in a sack and she deposited about a dozen eggs before expiring. I had to try all the known foods of the genus, but when the young larvae started to eat willow [*Salix* sp.], I knew what species I had. I reared six moths, four males and two females, the only ones in my collection. I have never seen the moth since. An interesting thing about the larvae was that part of them were green, as one might expect sphingid larvae to be, but the rest were vivid purple! *Callosamia promethea* used to be, apparently, our commonest Saturniid [at Sardinia], but I haven't seen a cocoon for years. However, a friend of mine, who lives some three miles northwest of town, told me last fall about the horrible creatures that were eating up his lilac [*Syringa vulgaris*] bush, and that he rapidly demolished all of them. His description sounded like *promethea* larvae, although they may have been [*Hyalophora*] *cecropia* (18 August 1977).

My own collecting experience has shown me how collecting spots have changed over the years, with the old plants and trees increasing in size, and new ones crowding in. Sometimes as those changes occur, moths formerly common disappear entirely. Other species, once quite common, seem to have disappeared everywhere. I can give an outstanding example in your family of butterflies. When I was a kid the second commonest butterfly around here was the one Holland called *Chrysophanus hypophlaeas*. . . . It was *everywhere* in gardens, fields and roadsides. I haven't even seen one now in many years. *Pieris rapae*, of course, was the commonest, and still is (15 June 1977).

It has been of interest to me that in recent years I have seen no signs of a number of species that were common, or even abundant [in my youth at Sardinia]. Using the nomenclature in Dr. Forbes' *Lepidoptera of New York and Neighboring States,* these would include *Papilio cresphontes,* the *Lycaena phlaeas americana,* . . . the similar but larger species *thoë, Euptoieta claudia, Brenthis selene myrina, Aglais l-album j-album,* and *Aglais milberti.* On the other hand, at least two species that I looked for in those days and never saw became quite common in later years, *Limenitis archippus*

and *Lethe portlandia*. This latter one was probably here all the time, for I have seen it only on bait spread for moths in early evening (12 July 1977).

Mr. Rupert's sister, Florence Rupert, still lives at Sardinia, New York.

ACKNOWLEDGMENTS

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JOURNAL

of the

LEPIDOPTERISTS' SOCIETY

11 March 1987

The object of the Lepidopterists' Society, which was formed in May, 1947 and formally constituted in December, 1950, is "to promote the science of lepidopterology in all its branches, ... to issue a periodical and other publications on Lepidoptera, to facilitate the exchange of specimens and ideas by both the professional worker and the amateur in the field; to secure cooperation in all measures" directed towards these aims.

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Cover illustration: First stage larva of *Natada nasoni* (Grote) (Limacodidae), from Dyar 1899, J. New York Entomol. Soc. 7:61–67. Suggested by Marc E. Epstein.

Journal of

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PRESIDENTIAL ADDRESS, 1986: UNEXPLORED HORIZONS—THE ROLE OF THE AMATEUR LEPIDOPTERIST

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During the past few years, members have voiced various concerns about our Society, its meetings, and the nature of some papers published in our *Journal*. Comments include: 1, The Society is only for professionals these days. 2, The papers presented at meetings are too technical—where are the informal field trip–slide show presentations of old? 3, Only specialists can read the *Journal*. 4, How can an amateur hope to contribute or gain anything from membership in the Society?

Before I respond to these comments, let us look at who is an amateur and who is a professional. One definition is that a person who is paid for his efforts is a professional, and a person who does the same job without being paid is an amateur. An alternative definition might be that a person with formal training (meaning a college degree) in entomology or zoology is a professional (in the context of our Society), while a person who lacks such training is an amateur. Perhaps it would be better to use the term lay person rather than amateur. By either definition, I am a lay person, as are many other folks sitting in this room. I am a scientist by training, but not formally trained as an entomologist or lepidopterist, and with one exception in the past, not paid to work only with insects.

Among the people in this room are physicians, dentists, lawyers, engineers, professors and teachers, scientists from various disciplines, housewives, individuals who simply like butterflies and moths, young people, students, and yes—a few paid professional entomologists. Our Society is composed of a very broad spectrum of disciplines and inter-

ests, and the membership as a whole is not much different from the sample here today.

In his 1984 Presidential Address at the Alberta Meeting, Lee Miller singled out the myriad contributions made by amateurs to the study of Lepidoptera. Many of the past giants in our field were not professional entomologists. Skinner was a physician, Scudder a librarian, Henry Edwards an actor, Lord Rothschild a banker, William Henry Edwards a coal baron, Bates a naturalist and explorer, Bean an artist, and the list goes on. All of these individuals had one thing in common— they were interested in nature. The term used in those days was naturalist. Amateur or professional had no meaning. A naturalist was simply a person who was interested in and observed nature, and most naturalists were self-educated. They learned by reading, observing, and conversing or corresponding with other naturalists. It's a shame this term has nearly fallen from use, at least in North America.

We here are all naturalists with a common interest in Lepidoptera. So let us call ourselves naturalists whose major interest is lepidopterology. The only differences among us are the degrees to which we pursue our common interest. Some of us are field people who delight in collecting or photographing butterflies and moths. Some of us pursue rearing and life-history studies. Some of us work with nomenclature and classification, the field of taxonomy. Others of us look at details of behavior, genetics, and molecular biology as they relate to Lepidoptera. A few of us dabble in each of these areas.

Now let us look for a moment at how science and the ways of doing science have changed in recent years. Two major discoveries, one each in the physical and biological sciences, have altered our approach to all scientific disciplines. In 1947, the year in which our Society was founded, the transistor was invented, and it subsequently evolved into the microcircuit chip and microelectronics. Microelectronics has given us the tools and the ability to construct analytical instruments that measure physical and biological processes to a degree of accuracy and sophistication undreamed of by 19th and early 20th century naturalists. In 1953, Watson and Crick proposed the double-helix model for DNA (deoxyribonucleic acid), and molecular biology was firmly established. Knowledge of DNA structure coupled with electronic instruments designed to probe and elucidate this structure led to the deciphering of portions of the genetic code, and to the birth of genetic engineering and biotechnology. Discoveries being made in molecular biology are changing our ways of looking at biological phenomena, and are even changing our thinking about what constitutes a species and how we approach taxonomy and nomenclature. This should explain why some

Journal articles and meeting papers appear abstract—we are caught up in a bioscience revolution. Today biotechnology is the frontier of the biological sciences.

Biotechnology and related research require extensive laboratory facilities and sophisticated instrumentation. Such facilities are normally associated with large universities and research centers. Thus only a limited number of specialists are equipped to undertake studies of Lepidoptera at the molecular level.

Now, what about the rest of us? Do we have any open frontiers, and if so, where are they? The answer is yes, they are all around us! While molecular biology, with all its sophisticated methods to probe the very nature of life, is giving us information about similarities and dissimilarities among insects based upon laboratory analysis, it tells us nothing about how those same insects behave in their natural environments.

At one time, many specialists thought that species of Lepidoptera could be separated positively based upon such morphological differences as color, wing maculation, and genitalic structure. More and more, we are finding out that this is not so. In the genus *Colias,* for example, the male genitalia are essentially identical and wing paterns are similar; yet in the field these butterflies clearly segregate into recognizable groups that we call species. On the other hand, individual colonies of *Erebia callias* in North America and *Erebia tyndarus* in the Old World exhibit clearly defined polymorphism in male genitalia, although wing maculation remains constant.

In the western United States, there is the *Speyeria atlantis* complex which may represent a single species with multiple subspecies, or numerous closely related but separate species. To date, even the molecular biology approach has failed to decipher this complex. In the long run, probably careful field observations of mated pairs of these butterflies along with rearing adults from ova will resolve the species-subspecies question. The foregoing are just a few examples of problems that require further study. There are hundreds of unsolved problems in the moths, and in both tropical and arctic fauna.

Our frontier is the field and our mission is to study how Lepidoptera behave in their natural habitats. From field observations, we now know in *Speyeria mormonia* that the unsilvered "clio" form is really only a form. Mixed pairs are regularly observed *in copulo*. On the other hand, we have yet to resolve the relation of the dark-disc *Speyeria atlantis electa* to the pale unsilvered-disc *Speyeria atlantis hesperis*. In many areas these two butterflies are sympatric. They were described over 100 years ago, and we still don't know their true taxonomic status. Are they varietal forms, subspecies, or species? There are many such prob-

lems just with the species found within the forty-eight contiguous States and southern Canada. Collecting in the arctic and the tropics is uncovering many more unanswered questions.

For many of us, our laboratory is the out-of-doors wherever butterflies and moths occur. Our experimental work is to observe how these insects behave in the field and to rear them so that their life stages become known. We need to know flight patterns, courtship behavior, and life histories. Maybe then we can solve some of the many unanswered taxonomic questions. Frequently collectors simply collect insects and check the species off on a list. We need to pay more attention to how lepidopterans behave in their natural environments.

This is an area where nearly all of us can contribute. The only equipment required is a good pair of field boots or shoes, notebook, pen, binoculars, camera, and for some a butterfly net and other collecting paraphernalia. In many cases, the camera and binoculars can be omitted. The final ingredients are patience and perseverance. We need to know and record where lepidopterans fly, how they perch, their courtship patterns, how they oviposit and upon what, and their behavior in general. If we go into rearing, we need to record what the eggs look like, what the larvae look like in each instar, what they eat and what portions of the host are consumed, what the pupae look like and where they are placed. Do the larvae overwinter, or is hibernation as ova or pupae? These are simple and basic questions, yet they remain unanswered for some common and widespread species. Most lepidopteran rearing requires only simple equipment. Some sort of rearing cage is desirable, a container for the larval foodplant, soil for species that pupate on or in the ground, and twigs or other substrates for species that pupate above ground.

One of the most famous behavioral entomologists was J. H. Fabre who is known for his book *Social Life in the Insect World*. Fabre was an impecunious French naturalist who observed insect life about his garden; he was too poor to travel, yet his work is renowned the world over. Of equal stature to Fabre is Theodore D. A. Cockerell, who at age 20 traveled from his native England to the Rocky Mountains of Colorado in the hope that his tuberculosis would be arrested. His hope was realized and he died at the age of 82, renowned as a naturalist, scholar, and ultimately a professor at the University of Colorado—all without a university degree.

What are the benefits of the studies mentioned above? They provide useful and very necessary information. It is only through such field observations that we will ultimately understand the complex relations among many lepidopterans. The side benefits are recreation and just being in the out-of-doors close to Nature and her wonders.

Now I would like to share with you some of the problem species that have intrigued me for the past several years. My major interests lie with the arctic and arctic-alpine fauna, and the examples which follow derive from these. First is the satyrid *Oeneis bore*. For many years, the taxa *bore* and *taygete* were considered to be separate species, and were so treated by dos Passos in his 1964 Synonymic List. About a decade later, a paper of his read at an annual meeting of our Society suggested that these two taxa are conspecific, and some subsequent lists have taken this approach. The basis used to separate *bore* and *taygete* related to whitish veining on the ventral hind wings, present in *taygete* while absent in *bore*, although male genitalia appear identical. As more arctic material became available for study, it was evident, based on the discovery of mixed populations, that the white veining was not a reliable character. The name *taygete* fell into synonymy under the older name *bore*. Based on my collecting in the Yukon and northern British Columbia in 1984 and 1985, it now appears that this situation is not so simply resolved. While it is true that the white-venation character is unreliable, there are clearly two phenotypes that fly together: one dusky and the other brightly colored. A casual observer, seeing only a few specimens, might simply write off these differences as normal variation within a geographic population. Series have been collected, however, at several locations in the Yukon and northern British Columbia. Flight patterns are different and no mixed-phenotype mated pairs have been observed. Opposite sexes of opposite phenotypes ignore one another. Preliminary examination of the male genitalia indicates no difference between the two color forms. In the field, the butterflies behave as two separate species; in the laboratory working with museum specimens, we would treat them as one species after applying the usual taxonomic methods.

Oeneis polixenes in the western arctic behaves in a similar manner. There is a dark phenotype and a pale one. I first collected two females of the dark form in a bog in eastern Alaska in 1971. At that time, I simply discounted these specimens as melanic aberrants. Several years ago, Jim Troubridge of Cayuga, Ontario, pointed out to me that this dark phenotype occurs only in odd-numbered years, while the paler typical *polixenes* is annual. His collecting led him to believe that the biennial dark form occurs at low elevations in forest bogs, while the normal form occurs in more open areas and on mountain tops. In some localities, both forms can be collected where there is a fairly abrupt transition from boggy forest to open grassy hillsides. In 1985, I found that the dark form is not restricted to low-elevation bogs when I collected a few examples on the summit of Pink Mountain in northern British Columbia. As is the case with *bore*, the flight patterns for the

two forms are quite different and I have not yet seen mixed pairs *in copulo*. No differences in male genitalia have been detected. The dark *polixenes* is found in parts of Alaska, the Yukon Territory, and northern British Columbia.

It is not surprising that paradoxes are turning up in the western Arctic. Until recently, collecting in this region was limited, and one is frequently inhibited by weather. New roads into previously uncollected areas, and collectors fortunate enough to encounter hot dry weather at the right time of year have resulted in the discovery of some fascinating yet perplexing butterflies. On the other hand, new species and subspecies have turned up in heavily collected parts of America; witness *Clossiana acrocnema* in 1978 along a heavily traveled hiking trail in southern Colorado, and *C. improba harryi* in 1982 in central Wyoming, also along a well traveled trail. Many surprises are turning up in Idaho, largely through the efforts of Nelson S. Curtis of Moscow, Idaho. Again we see the situation of differing phenotypes and voltinism of a supposed single species, this time in the *Coenonympha tullia* complex. In one area of Idaho, there appears to be a univoltine population on the wing between flights of bivoltine population. Only careful field observations (like those by Curtis) can elucidate this sort of situation. From museum material, one would simply infer an extended flight period of a single species.

Elsewhere in Idaho, traditional species concepts appear to break down. This situation is most evident in Valley Co., where among others, apparent hybrids or intergrades between *Speyeria atlantis* and *S. hydaspe*, *Euphydryas anicia* and *E. chalcedona*, and *Colias interior* and *C. pelidne* have been collected. The *Colias* population is particularly interesting in that instability of phenotype is the rule. Both wing shape and maculation vary widely. This population was first discovered by Jon Shepard of Nelson, British Columbia, and its geographic range has since been studied by Curtis and Ferris. It is not yet clear why Valley Co. fosters so many unusual butterfly phenotypes. The moths collected there have produced nothing unusual.

As a final example, we return to the Arctic and the *Colias hecla* complex. Several years ago, I described *Colias hecla canadensis* from Alberta and British Columbia. A somewhat similar butterfly occurs in the northern Yukon and sporadically in Alaska. It is not clear if two species are involved, or simply temporal forms of *C. hecla*. In the Ogilvie and Richardson Mts. in the Yukon, *hecla* that appear early in the season have pale-colored males with narrow wing borders, and females that are on the wing at the same time are usually white or very pale yellow with perhaps an orange flush. As the season progresses, brightly marked typical *hecla* appear in which the females are bright

orange-yellow and the males have broad dark wing borders. Are two species involved, or does climate play a role? Do the early-emerging adults represent perhaps last instars entering hibernal diapause while the later-emerging adults represent penultimate-instars at the time of hibernal diapause? Or does the early group of pale adults represent larvae that passed two winters, while the later-emerging bright specimens passed only one winter as larvae? Do climate and larval development at the time of diapause or pupation effect selective expression of adult color (leucopterin rather than xanthopterin in the females)? At this point, I cannot answer these questions. More fieldwork is needed and probably eventual rearing of adults from ova under controlled conditions.

Now we return to the questions posed at the beginning of this presentation. In short, how does the lay person fit into the Lepidopterists' Society today? I would suggest simply by being a naturalist. The frontier is still in the field as it was a century ago. We still have much to learn about familiar butterflies and moths, and even more to learn about species that occur in remote regions. Since the discovery of *Clossiana acrocnema* a few years ago, other new species described from North America only include *Oeneis excubitor*, *Erebia occulta* and *E. lafontanei*, and *Mitoura thornei*. There are undoubtedly other unknown species. There is also the enigma of *Erebia inuitica*, known from a single specimen. No amount of sophisticated laboratory work is going to uncover uncollected new species. Only a lot of leg work in the field will accomplish this. Laboratory instruments will not help us determine the geographic distributions of the many little-known butterflies and moths that occur in North America and elsewhere. In some tropical regions, species may become extinct without our knowing that they ever existed, owing to extensive destruction of virgin jungle and lack of collecting.

I have described a few unsolved problems that are of interest to me. In some cases, analytical methods derived from molecular biology *might* answer questions, but where they have been tried (in *Colias* and *Speyeria*) results so far are disappointing.

What we do need is more field naturalists studying behavior, life history, and producing distribution maps. Simply accumulating data but not sharing information is not enough. The contribution that a member of our Society can make to the group as a whole is by sharing discoveries. What the member then gains is the satisfaction of making a scientific contribution and extending our knowledge of the natural world.

Some members may suggest that they are too old or have physical disabilities and thus cannot conduct field studies. Yet I know of some

Society members who are in their eighties and still actively collecting in the field. Many years ago, I exchanged specimens with a collector in England, who sent me fine examples of British butterflies and moths. One day I received a letter from his mother informing me that my correspondent had died. He was in his early twenties and had been an invalid confined to a wheelchair, but undaunted by his physical condition he reared butterflies and moths from live material supplied by friends. So nearly anyone can contribute to lepidopterology.

In closing, I give you this challenge: the natural laboratory is waiting for you, whether it be your garden, the mountains, the prairie, the desert, the arctic or the tropics. The butterflies and moths are there. Go find out where they live and how they live, and then share your findings with the rest of us. You will have the satisfaction of knowing that you have made a contribution to your colleagues and that you have extended our knowledge of Lepidoptera. I wish you Godspeed.

SELECTIVE OVIPOSITION BY MONARCH BUTTERFLIES (*DANAUS PLEXIPPUS* L.) IN A MIXED STAND OF *ASCLEPIAS CURASSAVICA* L. AND *A. INCARNATA* L. IN SOUTH FLORIDA

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ABSTRACT. Host plant selection by ovipositing monarch butterflies occurred in a mixed stand of the milkweeds *Asclepias curassavica* and *A. incarnata* in a south Florida pasture. Three times more immature monarchs were found on *A. curassavica* than on *A. incarnata*. When these numbers were balanced for biomass differences between the two plant species, there were 5.7 times the number of monarch immatures/dry leaf mass/100 m² on *A. curassavica* than on *A. incarnata*. Since *A. curassavica* had 36 times more cardenolide than *A. incarnata*, we suggest that the basis for selective oviposition by monarchs is to provide an effective cardenolide-based defense for their offspring.

Only 27 of the 108 North American species of the milkweed genus *Asclepias* (Woodson 1954) have been recorded as larval food plants of monarch butterflies, *Danaus plexippus* L. (Table 1). This restricted use of host species may reflect host availability, or active host selection. If, as Dixon et al. (1978) suggest, ovipositing monarchs do not discriminate between milkweed species on the basis of their cardenolide content, the criteria that determine patterns of resource use are likely to be based on the abundance, temporal and spatial distribution, and habitat diversity of different *Asclepias* species. On the other hand, Brower (1961) found that ovipositing female monarchs in south central Florida selected *A. humistrata* rather than nearby *A. tuberosa* plants. Such host selection may well be influenced by variations in leaf biomass and morphology, qualitative and quantitative chemical defenses, and nutritive value, between *Asclepias* species, as Price and Willson (1976) have suggested for another milkweed feeding specialist.

Recent observations near Gainesville, north Florida, in spring 1983 and 1984, indicate that monarchs do not lay eggs on the common milkweeds *A. tuberosa* and *A. verticillata* and rarely lay eggs on two less common species, *A. amplexicaulis* and *A. tomentosa*. These four species have low cardenolide concentrations and are medium-sized to small plants (Table 2; Roeske et al. 1976). Two other common milkweed species, *A. humistrata* and *A. viridis*, are heavily exploited by ovipositing females from early April to June (Malcolm et al. 1987). Interestingly, these two milkweeds contain the highest concentrations of cardenolides and have the largest leaf biomass of the available species in north Florida (Table 2). Since monarchs are well known for their ability to store milkweed-derived cardenolides as a defense against

TABLE 1.   North American *Asclepias* species serving as hosts of monarch butterfly larvae in nature.

Asclepias species	Location	Reference
humistrata	Florida	Brower (1961, 1962), Nishio (1980), Cohen and Brower (1982), Nishio et al. (1983), Malcolm et al. (1987)
	Georgia	Nishio (1980), Nishio et al. (1983)
syriaca	Illinois	Price and Willson (1979)
	Michigan	Wilbur (1976), Malcolm and Cockrell, unpubl.
	New York	Rawlins and Lederhouse (1981), Malcolm and Cockrell, unpubl.
	Pennsylvania	Schroeder (1976), Malcolm and Cockrell, unpubl.
	Ontario	Beall (1948), Urquhart (1960), Malcolm and Cockrell, unpubl.
	Wisconsin	Barker and Herman (1976), Borkin (1982), Malcolm, Cockrell, Brower, and Brower, unpubl.
	North Dakota	Malcolm and Cockrell, unpubl.
	Minnesota	Malcolm and Cockrell, unpubl.
	Vermont	Malcolm and Cockrell, unpubl.
	Connecticut	Malcolm and Cockrell, unpubl.
	New Jersey	Malcolm and Cockrell, unpubl.
	Maryland	Malcolm and Cockrell, unpubl.
	Virginia	Malcolm and Cockrell, unpubl.
	Missouri	Malcolm and Cockrell, unpubl.
	Kansas	Malcolm and Cockrell, unpubl.
	Nebraska	Malcolm and Cockrell, unpubl.
	Iowa	Malcolm and Cockrell, unpubl.
	Ohio	Brower and Brower, unpubl.
viridis	Florida	Brower, Cockrell, and Malcolm, unpubl.
	Louisiana	Lynch and Martin, unpubl.
	Texas	Malcolm and Cockrell, unpubl.
	Arkansas	Malcolm and Cockrell, unpubl.
	Oklahoma	Malcolm and Cockrell, unpubl.
	Missouri	Malcolm and Cockrell, unpubl.
	Kansas	Malcolm and Cockrell, unpubl.
asperula	Texas	Malcolm, Cockrell, Lynch, and Martin, unpubl.
tomentosa	Florida	Brower, Cockrell, and Malcolm, unpubl.
obovata?	Louisiana	Malcolm and Cockrell, unpubl.
	Texas	Malcolm and Cockrell, unpubl.
curassavica	Florida	Brower (1961), this paper
incarnata	Florida	Brower (1961), this paper
	Kansas	Malcolm and Cockrell, unpubl.
	Wisconsin	Brower and Brower, unpubl.
longifolia	Louisiana	Riley, Lynch, and Martin, unpubl.
hirtella	Arkansas	Malcolm and Cockrell, unpubl.
	Missouri	Malcolm and Cockrell, unpubl.
viridiflora	Michigan	Wilbur (1976)
	Louisiana	Lynch and Martin, unpubl.
	Texas	Malcolm and Cockrell, unpubl.
	Kansas	Malcolm and Cockrell, unpubl.
amplexicaulis	Florida	Brower, Cockrell, and Malcolm, unpubl.
	Illinois	Price and Willson (1979)

TABLE 1.   Continued.

Asclepias species	Location	Reference
	Texas	Malcolm and Cockrell, unpubl.
	Louisiana	Malcolm and Cockrell, unpubl.
	Oklahoma	Malcolm and Cockrell, unpubl.
tuberosa	Florida	Brower (1961, 1962)
	Illinois	Price and Willson (1979)
	Michigan	Wilbur (1976)
verticillata	Illinois	Price and Willson (1979)
	Kansas	Malcolm and Cockrell, unpubl.
	Minnesota	Malcolm and Cockrell, unpubl.
exaltata	Michigan	Wilbur (1976)
	Virginia	Malcolm and Cockrell, unpubl.
variegata	Texas	Malcolm and Cockrell, unpubl.
purpurascens	?	Urquhart (1960)
	Kansas	Malcolm and Cockrell, unpubl.
lanceolata	?	Urquhart (1960)
	Florida	Brower, unpubl.
sullivantii	?	Urquhart (1960)
oenotheroides	Texas	Lynch and Brower, unpubl.
fascicularis	California	Dixon et al. (1978)
eriocarpa	California	Brower et al. (1982)
speciosa	California	Brower et al. (1984b)
californica	California	Brower et al. (1984a)
erosa	California	Brower et al., in prep.
cordifolia	California	Brower et al., in prep.
vestita	California	Brower et al., in prep.

predators (Brower 1984), cardenolides may be implicated in some form of host selection.

To test host selection by *D. plexippus* between *Asclepias* species, based on biomass and cardenolide measures, we counted the numbers of monarch eggs and larvae on plants within a mixed stand of two *Asclepias* species, *A. curassavica* and *A. incarnata*, that are known to have different cardenolide concentrations (Roeske et al. 1976).

METHODS

The study site was a large mixed stand of *A. curassavica* and *A. incarnata* in a wet pasture adjacent to a man-made lake 15 km NW of Miami, Dade Co., Florida (25°45′N, 80°22′W, near junction of highways US-27 and I-95). On 1 and 2 September 1984, six 10 m × 10 m, randomly selected plots were searched and the following measurements made: 1) number of plants per plot, 2) plant height, 3) number of stems per plant, 4) presence of flower buds and flowers (no seed pods were found), 5) number of leaf pairs per plant (like most milk-

TABLE 2.   Leaf cardenolide concentration and plant size of five milkweed species in May 1983 and 1984 within 25 km of Gainesville, Florida.

Asclepias species	Cardenolide concentration (μg/0.1 g dry leaf)				Mean dry leaf biomass/plant (g)
	Mean	SD	Range	N	
Common					
humistrata	471	157	182–797	29	7.8
viridis	478	136	316–676	7	12.5
verticillata	14	—	—	1	<0.1
Occasional					
amplexicaulis	3	3	0–6	4	1.2
tomentosa	15	12	6–23	2	1.8

weeds these two species have opposite leaves), and 6) numbers of monarch eggs and larvae by instar. All eggs were collected and kept until larval emergence to determine whether they were *D. plexippus* or the queen, *D. gilippus*. The three eggs on *A. curassavica* and one on *A. incarnata* that proved to be queens were excluded from the analysis. Arbitrarily selected leaf samples were also collected from five plants of each species to measure leaf length, width and dry weight. These dried leaves were ground, mixed, and 0.2 g of each species extracted with ethanol to estimate their cardenolide concentrations by spectroassay (Brower et al. 1975, 1984b).

RESULTS

The cardenolide concentration of *A. curassavica* leaves was 864 μg cardenolide/0.1 g dry leaf, and that of *A. incarnata* 24 μg cardenolide/ 0.1 g dry leaf. Thus *A. curassavica* at this location had, on average, 36 times more cardenolide than *A. incarnata*.

The six 100 m^2 plots contained 182 *A. curassavica* plants, with 430 stems on which 33 monarch immatures were found, and 77 *A. incarnata* plants, with 393 stems bearing 11 immature monarchs, distributed between the plots as shown in Table 3.

The two milkweed species are very similar in appearance, bearing similar sized, lanceolate leaves. Neither leaf length, width, or shape (length/width) of the two species were significantly different (Table 4a), but the dry leaves of *A. incarnata* were significantly heavier than *A. curassavica*. Since *A. incarnata* plants were significantly taller with more stems per plant than *A. curassavica* (Table 4a), they also had significantly more leaves (Table 4b). Thus each *A. incarnata* plant had greater biomass available to monarch larvae than *A. curassavica*. However there were more than twice as many *A. curassavica* than *A. incarnata* plants per 100 m^2 (Table 4b), which resulted in similar num-

TABLE 3. Distribution of immature monarchs on six 100 m² plots in a mixed stand of *A. curassavica* and *A. incarnata* near Miami, Florida, on 1 and 2 September 1984.

Plot no.	*Asclepias* species	No. plants	No. stems	Eggs	Instar no. 1	2	3	4	5	Total
1	*curassavica*	34	92	6	—	2	—	—	—	8
1	*incarnata*	13	86	1	—	—	—	—	1	2
2	*curassavica*	62	162	6	—	1	—	—	—	7
2	*incarnata*	16	89	—	—	—	—	—	—	0
3	*curassavica*	17	44	1	—	1	—	—	—	2
3	*incarnata*	8	43	—	—	1	—	—	—	1
4	*curassavica*	31	69	5	—	—	—	—	—	5
4	*incarnata*	6	36	1	—	—	—	—	—	1
5	*curassavica*	17	27	—	—	1	—	—	—	1
5	*incarnata*	18	66	—	—	1	—	—	—	1
6	*curassavica*	21	36	4	3	2	—	—	1	10
6	*incarnata*	16	73	5	—	1	—	—	—	6
Total *curassavica*		182	430	22	3	7	—	—	1	33
Total *incarnata*		77	393	7	—	3	—	—	1	11

bers of stems overall (Table 3, $t = 0.28$, $P = 0.78$ NS) with almost equal leaf density and dry leaf biomass of each *Asclepias* species available to ovipositing monarchs (Table 4b).

Despite the similarity of the leaf biomass for each milkweed species, three times the number of immature monarchs (eggs to fifth instars) were found on *A. curassavica* than on *A. incarnata* (Table 4b). Similarly, when numbers of monarch immatures are corrected for host biomass, there were more than five times the number of monarch immatures/dry leaf mass on *A. curassavica* than on *A. incarnata* (Table 4b).

The difference between the numbers of monarch immatures on the two *Asclepias* species is unlikely to be explained by flower attraction since significantly more *A. incarnata* plants (with fewer monarch immatures) were flowering than *A. curassavica* (Table 4b), although most plants of both species were flowering.

DISCUSSION

We suggest that our observation of significantly more immature monarchs/leaf mass on *A. curassavica* than on *A. incarnata* may be explained by the 36 times greater cardenolide concentration of *A. curassavica* over *A. incarnata*. These results contrast with those reported by Dixon et al. (1978) who suggest that monarchs oviposit on *Asclepias* species with the lowest cardenolide concentrations. They found that

TABLE 4.   Plant characteristics of *A. curassavica* and *A. incarnata* on six plots in a mixed stand at the study site near Miami, Florida, on 1 and 2 September 1984. Differences were tested at the 0.05 level.

a) Leaf measurements and plant height

Asclepias species	Leaf length (mm)	Leaf width (mm)	Leaf length/width	Leaf dry weight (mg)	Plant height (cm)	No. stems/plant
curassavica						
Mean	81.1	14.2	5.8	34	70.5	2.4
SE	2.5	0.6	0.2	2	1.1	0.1
N	20	20	20	20	182	182
incarnata						
Mean	91.6	15.1	6.3	55	91.1	5.1
SE	5.8	1.0	0.4	9	1.8	0.4
N	18	18	18	18	77	77
t	1.6	0.9	1.0	2.2	9.8	8.1
df	24	36	26	20	257	257
P	0.06	0.20	0.16	0.02	0.0001	0.0001

b) Mean plant measurements and monarch numbers per 100 m^2

Asclepias species	No. plants	Percent flowering	No. leaves/ plant	No. leaves/ plot	Leaf dry mass (g)	No. immature monarchs	No. monarchs/ leaf mass
curassavica							
Mean	29.2	64	35.2	1,143	38.5	5.5	0.17
SE	7.1	7	2.9	334	11.2	1.4	0.06
N	6	6	6	6	6	6	6
incarnata							
Mean	12.8	90	88.2	1,130	62.5	1.8	0.03
SE	2.0	5	8.3	190	10.5	0.9	0.01
N	6	6	6	6	6	6	6
t	2.2	2.9	6.0	0.03	1.6	2.2	2.2
df	6	10	7	10	10	10	5
P	0.03	0.01	0.001	0.49	0.07	0.03	0.04

D. plexippus laid more eggs on *A. curassavica*, with a cardenolide concentration of 56 µg/0.1 g dry leaf, than on *Gomphocarpus fruticosus*, with 63 µg cardenolide/0.1 g dry leaf. However, their cardenolide concentrations are too similar to reach any conclusion as to cardenolide-based oviposition preference, particularly as they are the same cardenolide determinations first reported as "approximate amounts ±50%" (Rothschild et al. 1975), and were not determined for the same plants used in their oviposition experiments. *Gomphocarpus fruticosus* is also an African milkweed species which casts doubt on experimental relevance, since monarch butterflies will only encounter recently introduced plants of this species in Australia. Using Australian *D. plexippus*, Zalucki and Kitching (1982) also found that females preferred to lay eggs on *A. curassavica* rather than on *A. fruticosa* (=*G. fruticosus*); but citing different published data on cardenolide concentra-

tions (Roeske et al. 1976), they suggested the reverse, that monarchs laid eggs on the milkweed species with most cardenolide.

The use of milkweed-derived cardenolides appears to be at least a partial defense against wild avian predators for adult monarchs over-wintering in Mexico (Fink & Brower 1981, Fink et al. 1983, Brower & Calvert 1985, Brower & Fink 1985). It is likely that monarchs in south Florida also benefit from cardenolide-based protection against bird predators, particularly as late summer bird migrants pass through south Florida.

Although we recently found that monarchs regulate their carden-olide concentrations by increasing or reducing the cardenolide concen-trations from their larval host plants, milkweeds such as *A. incarnata* have insufficient cardenolide from which monarchs can concentrate an effective cardenolide-based defense. For example, although mon-archs reared on *A. speciosa* can almost double their cardenolide con-centrations relative to those of host plants, from 90 to 179 μg/0.1 g (Brower et al. 1984b), this concentration is less than the concentrations in butterflies reared on other species of cardenolide-rich milkweeds. Roeske et al. (1976) found that adult monarchs reared from *A. curas-savica* reflect the high cardenolide concentration of their host leaves, in this case of 386 μg/0.1 g dry leaf, with a concentration of 319 μg/ 0.1 g dry butterfly. In contrast, they found monarchs reared from *A. incarnata* with 0–28 μg cardenolide/0.1 g had between 28 and 127 μg cardenolide/0.1 g dry butterfly. The emetic response of bird predators increases with cardenolide concentration above a lower threshold de-pendent on cardenolide polarity (Roeske et al. 1976). Thus monarchs that fed on *A. curassavica* as larvae at our site near Miami will be much better protected by cardenolides against bird predators than monarchs that developed on *A. incarnata*.

Since individual plants of both species have a mean dry biomass sufficient to support the development to pupation of at least one mon-arch larva (between 0.92 g and 1.74 g dry leaf is required [Schroeder 1976, Dixon et al. 1978]; *A. curassavica* has $0.034 \times 35.21 = 1.20$ g, and *A. incarnata* has $0.055 \times 88.23 = 4.87$ g [Table 4]) a monarch larva need not move from plant to plant, either within, or between the two milkweed species. Thus the effectiveness of cardenolide-based monarch defense is likely to be determined primarily by the oviposi-tion behavior of the adult female rather than by larval movements, particularly in view of the unpredictable costs and benefits of such larval movement between milkweeds (Borkin 1982). Unlike Borkin, we do not find instars 2 and 3 moving between plants in Florida. If late instars move between plants, they are more likely to find another *A. curassavica* plant. Their feeding experience may also ensure that they keep moving until they find another host plant of the same species.

Cardenolides are unlikely to be the sole determinant of host selection in these observations. Other explanations of the observed oviposition bias for *A. curassavica* include 1) females may in some way be able to perceive a nutritional superiority of *A. curassavica* over *A. incarnata* (Erickson 1973); 2) monarch females may be more attracted to the orange and yellow flowers of *A. curassavica* than the pink flowers of *A. incarnata* (however, in central Florida monarchs preferred to oviposit on the pink flowered *A. humistrata* compared to the orange flowered *A. tuberosa* (Brower 1961, 1962)); and 3) females may have responded to the number of plants available for each species (Table 3) rather than to the similar quantities of stems, leaves, and leaf biomass.

Nevertheless, whatever the explanation, the natural experiment described in this paper as well as the observations reported by Brower (1961, 1962) are evidence for the oviposition preference by monarch butterflies for cardenolide-rich milkweed species. We suggest that this choice may be the result of natural selection having favored a discriminatory mechanism allowing adult female monarchs to choose milkweed species that provide their offspring with a more effective cardenolide-based defense against predators.

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BIOLOGY AND IMMATURE STAGES OF *CITHERONIA SPLENDENS SINALOENSIS* AND *EACLES OSLARI* IN ARIZONA (SATURNIIDAE)

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ABSTRACT. *Citheronia splendens sinaloensis* and *Eacles oslari* occur in Cochise, Pima, and Santa Cruz counties in southern Arizona. Both species have one generation per year. The flight season of *E. oslari* extends from early June to mid-August, and the larval host plants include *Quercus* species. The flight season of *C. splendens* extends from July to mid-August, and the larval host plants include wild cotton, manzanita, and New Mexico evergreen sumac. The immature stages are described for the first time.

The citheroniine fauna of Arizona is unique in that all seven species are primarily of Mexican origin (Tuskes 1985). The biology of the two largest species, *Citheronia splendens sinaloensis* (Hoffmann) and *Eacles oslari* Rothschild, is poorly known. Ferguson (1971) illustrated the adults, summarized existing information, and indicated that their immature stages were undescribed. The purpose of this paper is to describe the immature stages of both species and to present additional biological and distributional information.

Citheronia splendens sinaloensis
(Figs. 1–4)

Citheronia splendens sinaloensis is the only member of the genus presently known to occur in Arizona. *Citheronia mexicana* G. & R. occurs just south of Arizona, in Sonora, Mexico. Although reported from Arizona before the turn of the century, there are no recent United States records. *Citheronia regalis* (F.) and *C. sepulcralis* (Druce) are common in the eastern or central United States but do not occur farther west than central Texas.

Until recently *splendens* was only known from a few locations in Arizona, and specimens were scarce (Ferguson 1971). Observations and collecting in southern Arizona during the past 15 years have improved our knowledge of this species. Recently, *splendens* was taken from the Baboquivari Mts. (Pima Co.) east through Santa Cruz and southern Cochise counties to Guadalupe Canyon in the Peloncillo Mts. along the Arizona–New Mexico border, a distance of approximately 250 km.

Adults were taken at lights from the first or second week of July to the second week of August, with peak emergence occurring in late July. Males appear at lights usually after 2300 h, and are collected sporadically until predawn. Females are seldom attracted to lights. Mating occurs between 0100 and 0330 h.

Males exhibit little variation in forewing pattern, except in the extent of the cream colored markings through the antemedial area. The hindwings show more variation than the forewings. Some specimens exhibit diffused white patches through the dark gray submarginal area. The basal area of the hindwings can be cream or dark gray. Male forewing length varies from 48 to 56 mm, averaging 53 mm (N = 21). Females are larger than males, with forewing length ranging from 59 to 70 mm, averaging 64 mm (N = 12). Although forewing markings are similar to those of males, the wings of females are broader and less pointed, and the cream colored markings on the hindwings are reduced to small patches.

Adults and larvae are usually associated with high desert arroyos containing wild cotton (*Gossypium thurberi* L.) (Malvaceae), and transitional areas where manzanita (*Arctostaphylos pungens* H.B.K.) (Ericaceae), and New Mexico evergreen sumac (*Rhus choriophylla* Woot. & Standl.) (Anacardiaceae) grow. Arizona black walnut (*Juglans major* Torr.) (Juglandaceae) is associated with canyon washes above 670 m, and is a possible but unconfirmed natural host. Wild cotton and manzanita are the two most commonly utilized host plants. Some populations are highly host specific and utilize only one species even though others are present. Ova are deposited on the underside of the leaves, either singly or in groups up to four.

On cotton, the larva rests on the upper surface of the leaf curled in a J shape, and appears similar to a bird dropping (Fig. 2). During the early instars, most feeding occurs in the evening. As the larva matures, it rests on the petiole of the leaf or stem, and feeds sporadically through the day. Once larvae become established on the host plant, they are often reluctant to feed on other host plant species. Larvae transferred from cotton to manzanita, or from California pepper (*Shinus molle* L.) to cotton, often refuse to feed or fail to achieve the size of wild specimens. There are five instars, and development is rapid, with pupation occurring in September. Before pupation the larva leaves the plant and burrows into the ground where it constructs a pupation chamber of soil.

Larval Description

The following larval description is based on material reared from ova deposited by a female collected at Pena Blanca Lake, Santa Cruz Co., Arizona. Larvae collected from Box Canyon (Pima Co.) were also examined. Twenty-two larvae were examined; preserved larvae are in the author's collection.

First instar. Head: Black, diameter 1.5 mm. **Body:** Ground color black with orange band (Fig. 3). Length 15 mm, width 2.2 mm. Dorsal and dorsolateral thoracic (T) scoli
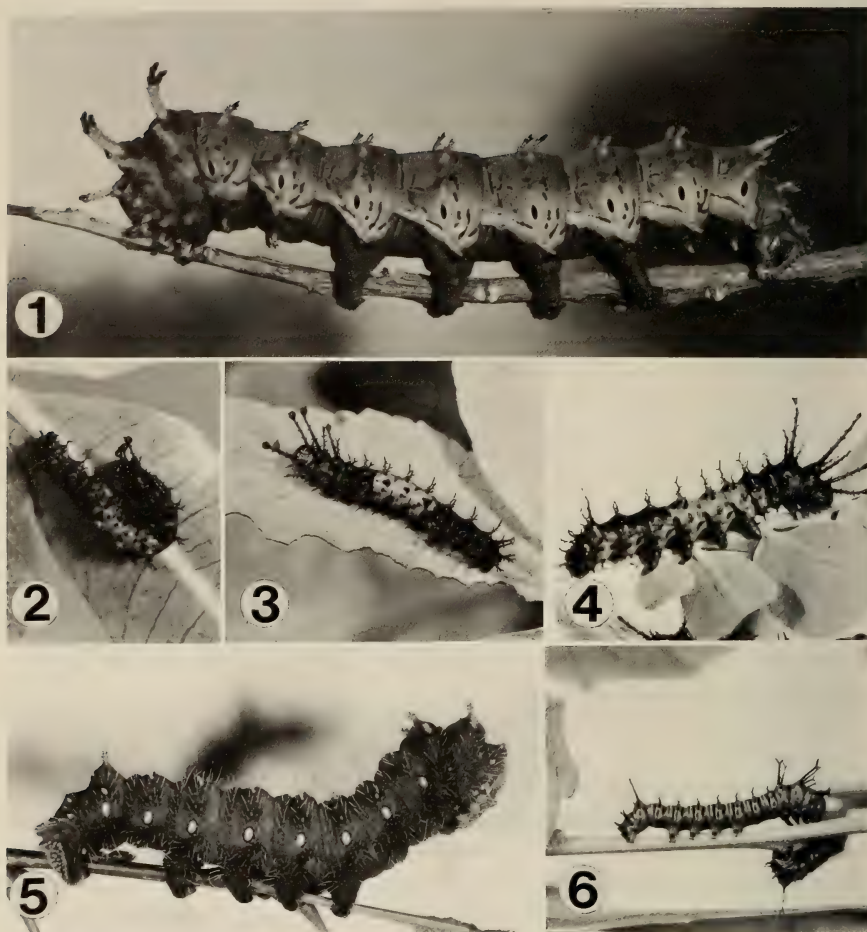
FIGS. 1–6.   1–4. Immature stages of *Citheronia splendens sinaloensis*. **1,** Mature fifth instar; **2,** First instar in bird dropping pose; **3,** First instar; **4,** Third instar. 5,6. Immature stages of *Eacles oslari*. **5,** Mature fifth instar; **6,** First instar.

black with bulb at tip, and 3–4× larger than dorsal abdominal scoli. Mid-dorsal caudal scolus on abdominal (A) segment 8 enlarged compared to dorsal abdominal scoli. All scoli black with short black spines on shafts. Segments A2, 6–8 with orange area on lateral surface surrounding each dorsolateral scolus. Segments A3–5 with orange extending from lateral surface dorsally over back; mid-dorsal black dot and smaller intersegmental black dot anterior to dorsal and dorsolateral scoli. True legs and prolegs black.

Second instar. Head: Black, diameter 2.1 mm. **Body:** Ground color black and orange. Length 24–26 mm, width 5 mm. Dorsal T2, 3 scoli 5× or greater in length than dorsal abdominal scoli. Mid-dorsal scolus (A8) 3× or greater in length than dorsal abdominal scoli. All scoli black with black spines on shaft. Segments A1–8: Lateral surface from just below lateral scoli to base of dorsal scoli orange. Orange coloration extending over mid-

dorsal area on A3–5, as in first instar, but more variable. Caudal segment, true legs, prolegs, and spiracles black.

Third instar. Head: Shiny black, diameter 2.5 mm. Clypeus black. **Body:** Ground color black or dark brown and orange (Fig. 4). Length 28–31 mm, width 6.7 mm. Dorsal thoracic and mid-dorsal scolus 2× or greater in length than abdominal scoli. All scoli black with short black spines on shaft. Thoracic segments primarily black. Abdominal segments: Area from base on lateral to dorsolateral scoli orangish brown. A series of black lines occurs on the lateral surface. Segments A1–8 with black line extending from just ventral of spiracle dorsally at 45-degree angle, terminating in intersegmental area. Segments A3–5: Orangish brown coloration extends dorsally over back. Circular black patch occurs between dorsal and dorsolateral scoli. Segments A1, 2, and 6–9 with black to dark brownish orange dorsal area. Segments A1–8 with 1–2 black lines extending from mid-dorsal area ventrally, terminating posteriorly to spiracle. Intersegmental area dark brown with black triangular patch in line with dorsal scoli. Ventral surface orangish brown, with numerous parallel black lines in intersegmental folds. True legs and prolegs black and orange. Spiracles black.

Fourth instar. Head: Black except for light brown frontal, frons, and adfrontal areas, diameter 4.6 mm. Clypeus cream. **Body:** Ground color dark purple to purplish pink. Length 59–66 mm, width 9.5–11 mm. Scoli of T2, 3 recurved, dorsal and dorsolateral 10.5 and 5.5 mm long, respectively. Dorsal scoli T1 straight, 7.5 mm long, shaft white with black tip; short black spines on shaft. Mid-dorsal A8 scolus elongated, 10.5 mm long, with black shaft and short black spines. Dorsal, dorsolateral, and lateral scoli black with short black spines on shaft. Base of all abdominal scoli orangish brown. Abdominal segments: Dorsal, dorsolateral, and lateral surfaces dark purple to purplish pink. Posterior and anterior portion of abdominal segments with 1–2 thin black vertical lines. Small black vertical line and 2 black dots occur between dorsal and dorsolateral scoli. Thoracic segments primarily black dorsally, lateral surface black to dark purple. Ventral surface purplish brown; intersegmental area with 1–2 thin parallel black lines. True legs black to light brown. Proleg lateral surfaces black to dark purple, anterior and posterior surfaces light brown. Spiracles black.

Fifth instar. Head: Shiny black, frontal suture brown, frons light brown, diameter 9.2 mm. Clypeus light brown. **Body:** Ground color pale purplish brown. Length 110–117 mm, width 15–17 mm. Dorsal and dorsolateral thoracic scoli T2, 3, and mid-dorsal scolus A8, 2× or greater in length than dorsal abdominal scoli. All dorsal, dorsolateral and lateral scoli light orange to light brown with black tips and small black spines on shaft. Sublateral scoli on T2, 3, and A7–9 light brown. Abdominal segments pale purplish brown. Intersegmental area light brown with thin black vertical lines. Cream colored undulating subspiracular fold extending from T3 to A8. Numerous thin black lines or dots on dorsal and lateral surfaces. One small black dot occurs anterior to dorsolateral scoli, and two between dorsal and dorsolateral scoli. T3–A8 with V-shaped mid-dorsal marking on each segment. Anterior to spiracle, black dots form continuous line to mid-dorsal area. Thin black line paralleling intersegmental fold. Ventral surface brownish black; intersegmental area with 1–2 thin parallel black lines. True legs light brown. Proleg lateral surface dark purple, anterior and posterior surfaces light brown. Spiracles black.

Mature larvae of U.S. *Citheronia* are readily distinguished from each other. Larvae of *splendens* (Fig. 1) have a purplish brown ground color. Dorsal and dorsolateral thoracic scoli are light brown at the base with black tips. There is a trace of a cream colored abdominal subspiracular line, and the ventral surface is brownish black. *Citheronia mexicana* occurs in Sonora, Mexico and has been reported from Arizona. Mature larvae of *mexicana* have a dark brown to black ground color and a prominent light yellow subspiracular line that extends the length of the abdomen. The dorsal and dorsolateral thoracic scoli are

light pink with black tips. Larvae of *regalis* have a brownish green ground color and bright red and black dorsal thoracic scoli. Bold white spiracular patches form a line on the lateral abdominal surface, but no subspiracular line is present. The ventral surface is greenish. Larvae of *sepulcralis* have a brown ground color and light brown dorsal and dorsolateral thoracic scoli. No spiracular or subspiracular white or cream colored lines or patches are present on the lateral surface, and the ventral surface is brown. Neither *regalis* or *sepulcralis* occur west of central Texas and are thus allopatric relative to *splendens*.

Eacles oslari
(Figs. 5, 6)

Eacles from southern Arizona was assumed to represent a disjunct population of *Eacles imperialis* (Drury) until Ferguson (1971) elevated it to species status, based on differences in distribution, adult morphology, coloration, and pattern. At that time, *E. oslari* was rare in collections, and only 16 specimens were available for examination, all of which were from the Nogales–Pena Blanca Lake area of Santa Cruz Co., Arizona. Since then, *oslari* has been found in lower Madera Canyon and Box Canyon in southern Pima Co., and in Patagonia, and most of the major canyons in the Huachuca Mts. of western Cochise Co. It is also widespread in Sonora and Sinaloa, Mexico. Although previously unreported from Mexico, *oslari* appears to be primarily a Mexican species whose northern limits extend into southern Arizona.

The flight season of *oslari* in Arizona extends from the first week of July to mid-August, but the peak flight period is from 20 July to 5 August. Both sexes are attracted to lights, but males are more frequently captured than females. Forewing length of males ranges from 51 to 58 mm, averaging 56 mm (N = 27); females are larger, forewing lengths ranging from 64 to 68 mm, averaging 66 mm (N = 38). There are three distinct adult color phenotypes resulting from differences in ground color: (1) deep yellow, (2) orangish brown, or (3) pale lavender to lavender-tinged. Some specimens appear transitional; yellow is the most common phenotype.

In captivity, females deposit ova singly or in clusters of up to six. Confirmed larval food plants are *Quercus oblongifolia* Torr. Mexican blue oak, and *Q. emoryi* Torr., Emory oak, but other species of oak are probably utilized. Early instars are brown; after the third instar, larvae may be either brown or green. Before pupation, the larva leaves the tree and constructs a pupation chamber underground. In captivity, larvae have been successfully reared on various species of oak, California pepper tree, *Schinus molle* L. (Anacardiaceae), and *Liquidambar styraciflua* L. (Falatingiaceae). There is one generation per year.

Pine, a common host for *E. imperialis nobilis* Neumoegen, *E. imperialis pini* Michener, and some southern populations of nominate *imperialis*, appears unsuitable as a host for *oslari*. An attempt was made by Gage (1976) to rear 40 *oslari* from ova on various conifers, but only one larva reached the last instar. Although the larva was illustrated in color, the immature stages were not described.

Hybridization studies conducted by the author support the species rank assigned to *oslari* based on morphological criteria (Ferguson 1971). A newly emerged *imperialis nobilis* female, reared from ova collected in Waller Co., Texas, was tied out in Box Canyon, Pima Co., Arizona. The female attracted and mated with a male *oslari* at 0130 h, and the pair remained together until the following evening. Only 21 ova were deposited by the female. Seventeen were infertile, four developed embryos, but only one hatched, and it perished in the first instar.

Larval Description

The larval description is based on material reared from ova deposited by a female collected at Pena Blanca Lake, Santa Cruz Co., Arizona. Larvae reared by the author from females captured at Patagonia, Cochise Co. (N = 14) and Lower Madera Canyon, Pima Co. (N = 22) were also examined and are in the author's collection.

First instar. Head: Yellow with short light brown setae present, diameter 1.8 mm. **Body:** Ground color brown (Fig. 6). Length 11–13 mm, width 2.7 mm. Dorsal abdominal scoli black with small spines on shaft and one on apex. Dorsolateral and lateral scoli black with 1–2 black spines on shaft. Sublateral scoli on T1–2 and A6–7 consisting of short, simple black spines. Thoracic segments with enlarged dorsal and dorsolateral scoli which have forked tips. Mid-dorsal caudal scolus on A8 black with forked tip, at least 3× larger than dorsal abdominal scoli. Abdominal segments with 2 dark brown lines extending from lateral surface dorsally over back. Small crescent shaped line occurs anterior and ventral of spiracle. Ventral surface brown. True legs dark brown to black. Prolegs brown with black shields.

Second instar. Head: Diameter 2.7–3.0 mm. Black, frontal area near mandibles orange. Short black secondary setae present. Diameter 2.7–3.0 mm. **Body:** Ground color dark brown. Length 20 mm, width 4.5 mm. Dorsal, dorsolateral, and lateral abdominal scoli cream to brown with 1–4 black spines. Enlarged mid-dorsal caudal scolus with light brown shaft and numerous short black spines. Dorsal and dorsolateral thoracic scoli orangish brown to light brown with numerous short black spines on shaft; 2 black spines at tip of each scoli. Lateral abdominal surface dark brown with numerous light brown secondary setae. Thoracic segments dark brown. Ventral surface brown. True legs orangish brown. Prolegs brown with black shields. Spiracles black.

Third instar. Head: Brown, area adjacent to adfrontal region light brown. Short brown secondary setae present. Diameter 3.7–3.9 mm. **Body:** Ground color brown or green. Length 25–28 mm, width 6.2 mm. Enlarged dorsal and dorsolateral thoracic scoli red with short red spines. All abdominal scoli cream; short cream spines with black tips on shafts. Enlarged caudal scolus red with red spines on shaft. Anal shield light brown with bluish black center; numerous small raised circular blue or white spots present. *Green form:* Spiracles turquoise and ringed with black. Proleg green; shields brown. True legs light brown. *Brown form:* Spiracles black and ringed by an inner gray and outer black line. Prolegs dark brown; black shields. True legs light brown. Both color forms with

elongate setae present on dorsal and dorsolateral areas, short secondary setae on lateral surface and prolegs.

Fourth instar. Head: Dark brown or green, depending on body ground color. Light brown line extending from antennae, tapering dorsally to vertex of each lobe. Diameter 5.5 mm. **Body:** Ground color brown or green. Length 41–51 mm, width 10 mm. *Brown form:* Enlarged dorsal and dorsolateral thoracic scoli brownish purple, with short yellow spines on shaft. Dorsal abdominal scoli yellow with short black spines. Dorsal, dorsolateral, lateral, and sublateral scoli light yellow and greatly reduced in size. Mid-dorsal caudal scolus brownish purple and enlarged. True legs light brown. Prolegs brown. *Green form:* Ground color green. Other coloration as above with following exceptions. Enlarged dorsal and dorsolateral thoracic scoli yellowish. True legs yellowish. Prolegs green. Both forms with elongated setae on dorsal and dorsolateral area, short secondary setae on lateral surface and prolegs.

Fifth instar. Head: Brown or green depending on body ground color. Light brown line extending from antennae, tapering dorsally to vertex of each lobe. Diameter 7.8 mm. **Body:** Ground color brown or green (Fig. 5). Length 90–110 mm, width 18 mm. *Brown form:* Dorsal and dorsolateral meso- and metathoracic scoli enlarged, 2.5 mm long, pinkish beige with small yellow tubercles on shaft. Dorsal, dorsolateral, lateral, and sublateral abdominal scoli reduced, 1 mm long, ivory in color with 2–4 short spines. Enlarged mid-dorsal caudal scolus pinkish beige with small yellow tubercles on shaft. Ventral and lateral surface brown, dorsolateral and dorsal areas light brown to brownish pink. *Green form:* As above but ground color green. Both color forms with elongate setae 9–11 mm long on dorsal surface. Lateral and ventral surfaces with light brown to short white secondary setae. Prothoracic shield yellowish green, ringed with light brown tubercles. Anal shield dark blue to black with small, raised light blue or white circular spots; shield ringed with light orange; caudal proleg shield similar. True legs yellowish brown. Spiracles turquoise.

Larvae of *oslari* are similar in appearance and size to those of *imperialis* from the eastern U.S. Larval variation among *imperialis* populations (Michigan, Virginia, Florida, Mississippi, and Texas) is so extensive that characters which appear to make *oslari* larvae unique are also found in *imperialis*. The larvae of *oslari* tend to have less contrasting differences in ground color on the dorsal and lateral surfaces, and the spiracles are consistently turquoise. Most populations of *imperialis* have cream colored spiracles—others black or turquoise—and contrasting light brown patches on the lateral surfaces.

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NEW GENERA FOR THE NEOTROPICAL *"PAREROMENE"* SPECIES (PYRALIDAE: CRAMBINAE)

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ABSTRACT. Three new genera of neotropical diptychophorine Crambinae, *Cleoeromene*, *Neoeromene* and *Incaeromene*, are established to contain seven species hitherto listed under *Pareromene* Osthelder (a synonym of the Old World genus *Glaucocharis* Meyrick), and two new species. *Pareromene smithi* (Druce) is transferred to *Cleoeromene*. *Pareromene felix* (Meyrick), *P. herstanella* (Schaus), *P. octavianella* (Zeller), *P. parvalis* (Walker), and *P. straminella* (Zeller) are transferred to *Neoeromene*, while *N. parvipuncta* from Brazil is described as new. *Pareromene excitata* (Meyrick) was concluded to be synonymous with *P. parvalis*, and *P. leucanthes* (Meyrick) with *P. felix*. *Incaeromene* accommodates the single species *subuncusella* described as new. Two species groups are recognized within *Neoeromene* and their relations are briefly discussed.

Seven neotropical species of diptychophorine Crambinae which were correctly removed from *Diptychophora* Zeller by Błeszyński (1967) are still listed in *Pareromene* Osthelder. They cannot be retained under this name because it is synonymous with *Glaucocharis* Meyrick, a genus confined to the Old World (Gaskin 1985). Furthermore, all differ from *Glaucocharis* in significant morphological characters. While the whole group probably had a common origin, there is no question of the neotropical forms being congeneric with either *Glaucocharis* or *Diptychophora*. The latter genus was recently revised (Gaskin 1986).

Objectives of the present paper are to establish three new genera representing the lines of evolutionary divergence evident in the morphology of these neotropical forms, to describe two new species, to give two new synonymies, to illustrate characters not previously published for the known species, and to summarize features that distinguish the new genera from other genera of diptychophorine Crambinae.

If experience with Old World diptychophorines is any guide, neotropical genera of these small and inconspicuous moths are probably undercollected at present. Cladograms based on present knowledge probably would not fairly represent the true diversity of existing species. Nevertheless, on balance of apparent apomorphies, *Cleoeromene* and *Incaeromene* represent derivative lines from *Neoeromene*-like stock with unspecialized and specialized valvae, respectively. Within *Neoeromene* itself, two sets of trends can be recognized in male genitalia. The *parvalis* group (*parvalis*, *herstanella*, *octavianella*), with apically cleft uncus, strongly developed segregation of the sacculus, and aedeagus cleft apically into a pair of strong protrusions, seems to be more derivative than the *felix* group (*felix*, *straminella*), where the uncus is

entire, the sacculus only weakly segregated, and the aedeagus has simple apical sclerotization. I do not separate these lines into named genera because *parvipuncta,* with a slight medial depression at the apex of the uncus, a partially segregated lobe of the sacculus, and paired patches of apical sclerotization of the aedeagus not drawn out into actual protrusions, seems to provide a clear link between the two group-trends genitalically.

The following abbreviations are used in the text: BMNH (British Museum [Natural History]), CM (Carnegie Museum of Natural History, Pittsburgh), CNC (Canadian National Insect Collection, Ottawa), MCU (Museum of Cornell University), MNHU (Museum für Naturkunde der Humboldt-Universität, Berlin, German Democratic Republic) and GC (Private collection of the author). Specimens examined bear Gaskin and Shaffer determination labels (BMNH). In descriptions of male genitalia the LMB ratio refers to the length to median breadth ratio of the aedeagus. Decimals indicate position as a proportion of the total length of a structure or organ. In the forewing, measurements along the costa are taken from the base, those along the termen or margin from the apex, and those along fascia from the costa. In male genitalia, measurements along the uncus, gnathos, valva, valval costa and aedeagus are from the base of each. In female genitalia, measurements along the ductus bursae are from the ostium.

Key to the Genera of New World Diptychophorine Crambinae

1   Forewing vein R_3 vestigial or absent, hindwing M_2 absent (both sexes). Lateral, medial foramen present in vinculum of male _____ *Microcausta*
–   Forewing vein R_3 and hindwing M_2 fully developed. Male vinculum without foramen _____ 2
2(1)   ♂: Gnathos strongly "fish-hooked"; valva quadrate, truncated, barely as long as wide.
        ♀: Antrum membranous, simple _____ *Diptychophora*
–   ♂: Gnathos slightly curved or nearly straight. Valva about 1.5× longer than wide, often tapered apically.
        ♀: Antrum sclerotized, often complex _____ 3
3(2)   ♂: Juxta with two pairs of sclerotized apical horns.
        ♀: Antrum with complex folds but not segregated into laterally paired structures
_____ *Steneromene*
–   ♂: Juxta simple to complex, but without two pairs of protrusions.
        ♀: Antrum complex, with strong tendency for division into right and left lateral structures, including subantral accessory sacs _____ 4
4(3)   ♂: Juxta with huge medial spur. Gnathos hastate. Aedeagus lacking sclerotization.
        ♀: Antrum with pair of internal lateral cupped folds. Corpus bursae with two signa _____ *Cleoeromene*
–   ♂: Juxta lacking spur. Gnathos not hastate. Aedeagus with some apical sclerotization, often laterally divided.
        ♀: Antrum with a pair of internal lateral folds, but not cupped. Corpus bursae asignate _____ 5

5(4) ♂: Tegumen simple, uncus without basal spurs.
      ♀: As in 4 .... *Neoeromene*
  –   ♂: Tegumen with prominent apical posteriad spur. Uncus with 2 dorsal spurs.
      Female not known .... *Incaeromene*

Cleoeromene, new genus

Type species *Diptychophora smithi* Druce (1896:292, pl. lxiv, fig. 20) (by monotypy).

Description. Forewing Sc concurrent with R_1, R_3 and R_4 stalked. Hindwing cell nearly closed by connections between M_1, M_2; M_3 and Cu_1 arising from cell, but with roots close together. Male juxta bearing at its ventroposterior center a gigantic apically serrated, flattened prong. Valva tapering, with subapical prong arising from distal extremity of a saccular fold, but involved with costal region by introrse movement. Female antrum characterized by a pair of large, strong, lateral, internal, elongate cupped folds. Corpus bursae with two small circular signa.
Etymology. Κλέοσ (Kleos)—glory (Doric Greek); Ερωμένη (Eromenē)—mistress (f).

Cleoeromene smithi (Druce), new combination

Diptychophora smithi Druce (1896:292).
Diptychophora smithi Druce; Błeszyński & Collins (1962:299).
Pareromene smithi (Druce) Błeszyński (1967:92, 96).

Description (Fig. 1). Wing expanse 15–17 mm (N = 11). External features satisfactorily described by Druce (1896).
Male genitalia (Fig. 9) (N = 1). Uncus simple, swollen dorsally from 0.3–0.9. Gnathos tapering abruptly to slender pedicel, with spatulate-hastate, flattened apical expansion. Tegumen simple, with strong ventral margins. Vinculum narrow, barely half as wide in profile as length of uncus. Saccus narrow, elongate, almost tubular with rounded apex; equal in length to uncus. Juxta a quadrate plate, basally triangular, rounded apically, with concave lateral margins. A huge prong arising from upper central region of juxta, grotesquely out of proportion to rest of genitalia, nearly 4× length of uncus, is apparently formed of two fused elements and probably anellar or transtillar in origin. Valva rounded, tapered, with some centrobasal development which cannot be attributed for certain to development of the dorsal margin of the sacculus or ventral margin of the valvula region. Costa strong, drawn apically into short, blunt prong. Valvula with longitudinal medial pleat. Aedeagus about 1.2× length of valva, tubular, LMB ratio about 10:1, apically truncate, lacking cornuti or external spines.
Female genitalia (Fig. 10) (N = 1). Anal papillae weakly fused dorsally. Anterior apophyses about 0.6×, and 8th tergite about 0.5× length of posterior apophyses. Antrum a wide, flared funnel. Lamella antevaginalis highly sclerotized, developed into a pair of lateral, elongate, cupped plates curved below ostium (possibly forming a receptacle for the juxtal spur of the male). Lamella postvaginalis forming a strong, single, dorsal plate. Ductus bursae about 2.5× length of posterior apophyses. Scobinate subantral sac present at about 0.3, ductus seminalis joining at about 0.7. Corpus bursae bearing two small, circular signa.
Types. Lectotype ♂ (designated here), MEXICO: Amula, Guerrero, 6,000 ft (1,829 m), "August", Smith, BMNH, genit. prep. pyral. 15101. Paralectotypes: 5 ♂ with same data, 2 ♂ similar but "September", all BMNH.
Other material examined. MEXICO: 2 ♂, 1 ♀, Iguala, Guerrero, 2,400′ (731 m), 8.VIII.1954, J. G. Chillcott, CNC, genit. prep. D.E.G. 1979/3.

Discussion. Little is known about this species, other than that it inhabits moderate altitudes in SW Mexico. The relations to *Neoeromene* in genitalic characters in both sexes are clear, except that in *smithi* it is the juxta, rather than the valva, which has undergone
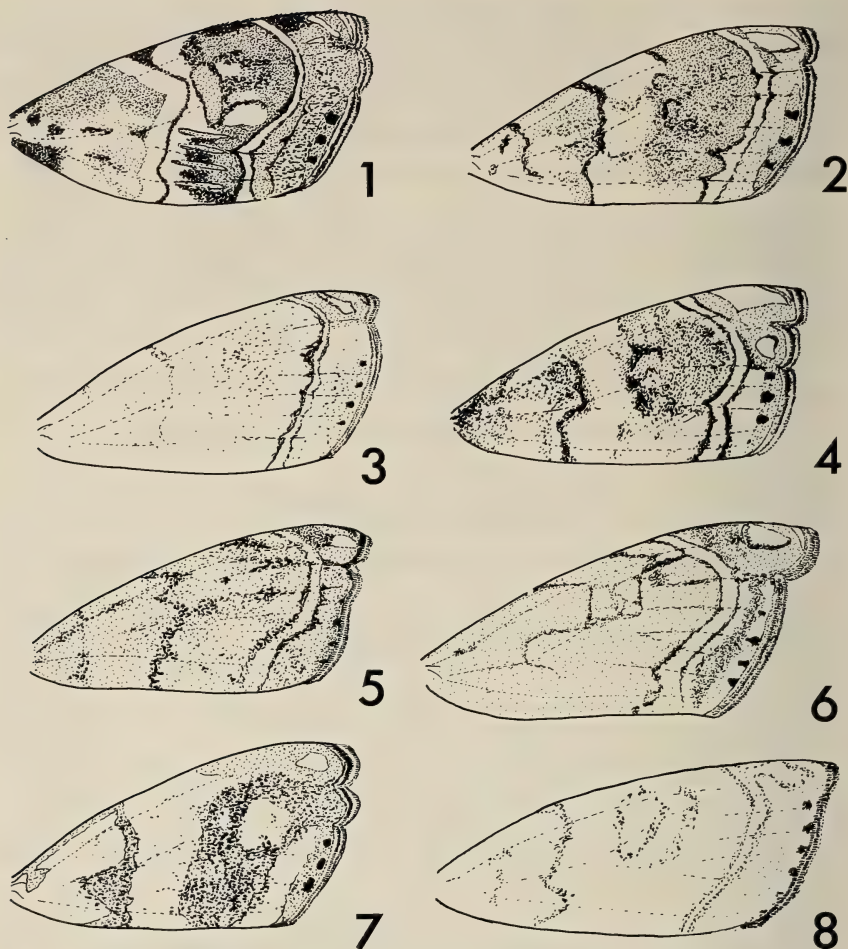
FIGS. 1–8. Forewings of *Cleoeromene*, *Neoeromene* and *Incaeromene* species. **1**, *Cleoeromene smithi*; **2**, *Neoeromene octavianella*; **3**, *N. herstanella*; **4**, *N. parvalis*; **5**, *N. parvipuncta*; **6**, *N. straminella*; **7**, *N. felix*; **8**, *Incaeromene subuncusella*.

sclerotized elaboration and differentiation. The antrum is also more complex in *Cleoeromene* than in *Neoeromene*.

Neoeromene, new genus

Type species. ?*Isopteryx parvalis* Walker (1865:1316).

Description. Forewing Sc concurrent with R_1; R_3 stalked with R_4; venation similar to *Glaucocharis* Meyrick. The male genitalia of *Neoeromene* characteristically have one or more large, sclerotized areas or spurs at the apex of the aedeagus, unlike any found in species of *Glaucocharis*. In about half the known species, the sacculus of the valva is
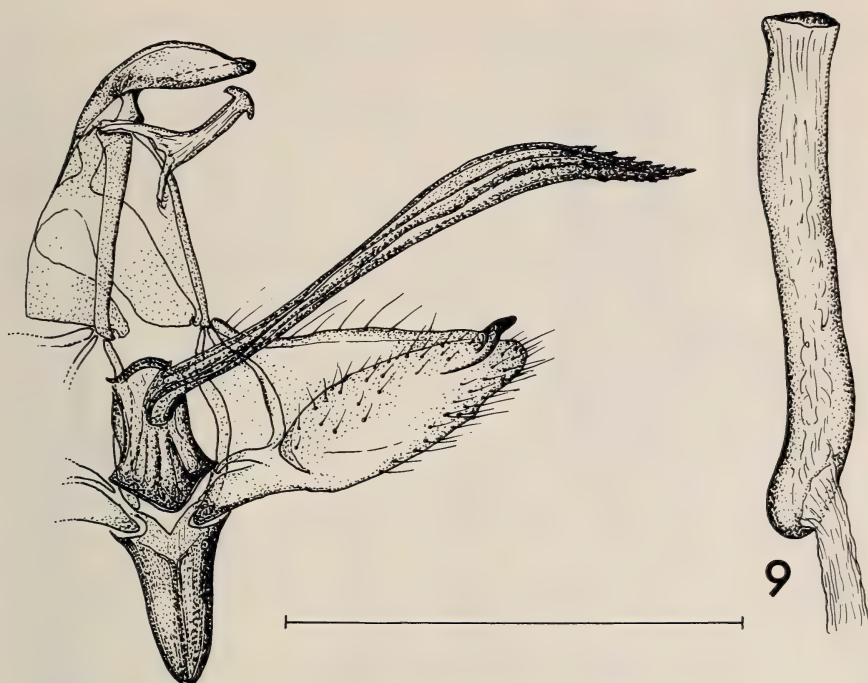
FIG. 9. Male genitalia of *Cleoeromene smithi* lectotype, posterior aspect with left valva (left), aedeagus (right). Scale = 1 mm.

strongly developed, with medial and ventral flanges or points or both. In the others, lateral or medial grooving of the valva extends from this region. In most species, the tip of the uncus is minutely or distinctly bifid. There is a strong tendency in all species for marked medial constriction of the juxta, for development of apical curved horns on the juxta, and the parallel development of an anellar structure around the aedeagus not found in *Glaucocharis*, but similar to that in some southern hemisphere Chilonini (Gaskin 1973). Relatively few females of *Neoeromene* are known, but in these the antrum is usually much broader and more complexly folded than in *Glaucocharis*, and the ductus is also broad and either pleated or laterally lobate. While the forewing markings are superficially similar to those of many species of *Glaucocharis*, there are marked differences and developments in the morphology of the genitalia which do not at all resemble those found in the Old World genus. Because females of several species are not known, the sexes are keyed separately.

Etymology. Νέοσ (Neos)—young; Ερωμένη (Eromenē)—mistress (f).

Key to the Species of Male *Neoeromene*

1 Costal region of valva strong or weak, but lacking basal protuberance; saccular region of valva differentiated into strong lobe terminating in a ventral prong 2

– Costal region of valva with prong; sacculus undeveloped 4

2(1) Sclerotization of sacculus confined to ventral margin 3

– Sclerotization extending thickly at right angles into middle of valva from base of terminal prong .... *octavianella*
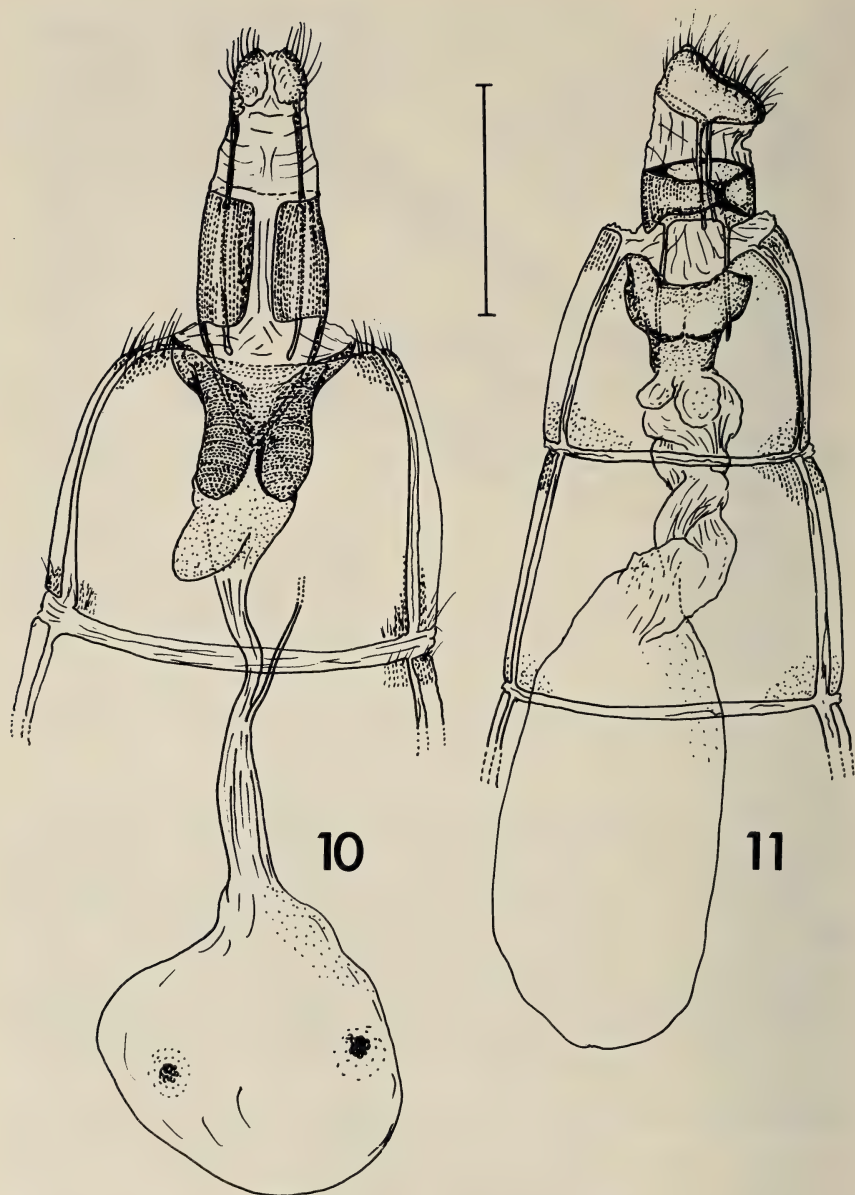
FIGS. 10, 11.   Female genitalia of *Cleoeromene* and *Neoeromene*, ventral aspect. **10,** *Cleoeromene smithi*; **11,** *Neoeromene parvalis*. Scale = 1 mm.

3(2) Terminal prong of sacculus short, barely 0.15× length of uncus; sclerotized anellar structure present in association with juxta _____ *parvalis*
–   Terminal prong of sacculus long, 0.5× or more length of uncus; membranous anellar structure present in association with juxta _____ *herstanella*
4(1) Costal prong smooth, arising near base, directed dorsoposteriad _____ 5
–   Costal prong heavily spinose, arising at about 0.5 and curving introrse and ventrad _____ *parvipuncta*
5(4) Juxta with pair of strong apical horns. Aedeagus with single narrow, apical prong _____ *straminella*
–   Juxta lacking apical horns. Aedeagus with large, flattened, sclerotized apical spur, with serrated edge and secondary hooked basal structure _____ *felix*

Key to the Species of Female *Neoeromene*

1   Medial depression in posterior margin of 7th sternum; antrum a strong, globate funnel, ductus bursae with several small accessory pockets in subantral region; corpus bursae massive _____ *parvalis*
–   Posterior margin of 7th sternum without medial depression; antrum strong, but not globate; ductus bursae without accessory pockets, or if present, associated with very elongate, narrow ductus bursae _____ 2
2(1) Ductus bursae less than length of 8th tergum at antrum, barely wider than apophyses at midpoint, elongate, and sclerotized only in antral region _____
_____ *herstanella*
–   Ductus broad, 2× length of 8th tergum at antrum, strong to about 0.4, with series of longitudinal pleats from subantral region to junction with ductus seminalis _____ *felix*

Neoeromene parvalis (Walker), new combination

?*Isopteryx parvalis* Walker (1865:1316).
Diptychophora excitata Meyrick (1931:109). **NEW SYNONYMY.**
Diptychophora excitata Meyrick; Błeszyński & Collins (1962:297).
Pareromene excitata (Meyrick) Błeszyński (1967:92, 96).
[?*Isopteryx parvalis* (Walker) Błeszyński & Collins (1962:296, 298), erroneously synonymized with *Diptychophora azanalis* (Walker).]
Pareromene parvalis (Walker) Błeszyński (1967:92, 96).

Description. Alar span 10–12 mm (Fig. 4) (N = 7). Redescribed here, since Walker's account is ambiguous. Labial palpi, head, thorax, abdomen, dull white, with scattered brownish scaling. Ground color of forewings dull white. Basal fascia nearly obsolete, position marked only by broken patches of dark scales. Antemedial fascia more complete, but solid, irregular, dark brown. Faint orange reniform marking present. Costa with large patch of white from median line to 0.6, terminated by short oblique bar on costa. Region between basal and antemedial fascia, and all of discal area, filled with scattered scales of buff proximally, darker brown distally. Postmedial fascia cream, irregularly and narrowly bounded with dark brown. Terminal zone creamy white, with faint orange stripe along margin, within which is a row of 3–4 irregular black spots. Apical zone faint orange, with large central white area. Cilia pale brown with dark apices. Hindwings creamy white, cilia similar, but with dark bases in apical region. Ventral surfaces straw and mid-brown, with apical forewing markings repeated from dorsal surface.

Male genitalia (Fig. 12) (N = 3). Uncus broad, simple, convexly tapered to a cleft apex. Gnathos slender, curved dorsad to bluntly pointed apex. Tegumen simple; vinculum a narrow strap at base of valva; saccus almost negligible; juxta basally triangular, sharply constricted distally into a narrow folded groove having membranous extensions with sclerotized margins, forming a weak anellar structure supporting aedeagus. Valva 2.7–3.0× length of uncus, apically broadly rounded; costal region a narrow sclerotized zone; sacculus a strong marginal lobe comprising basal ⅓ of valva, terminating in short, sharp
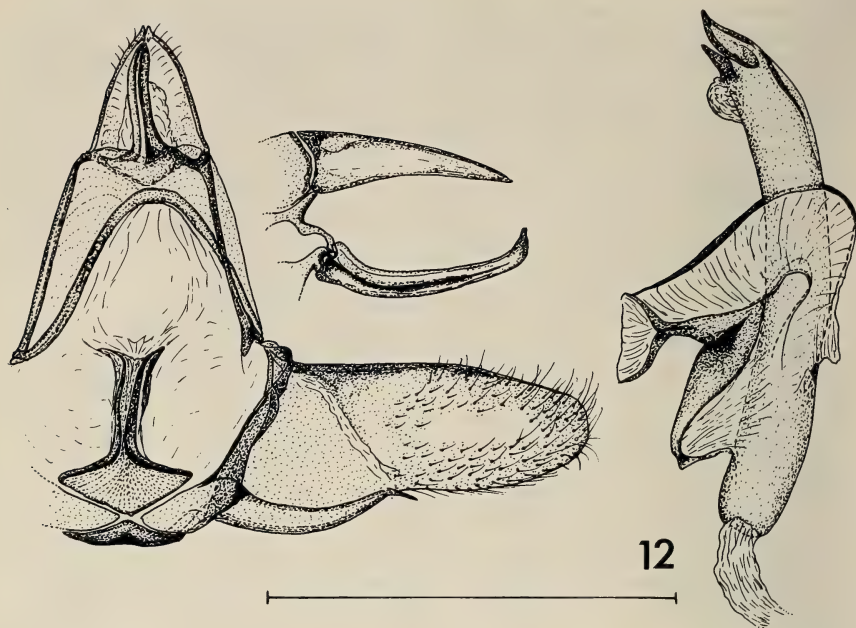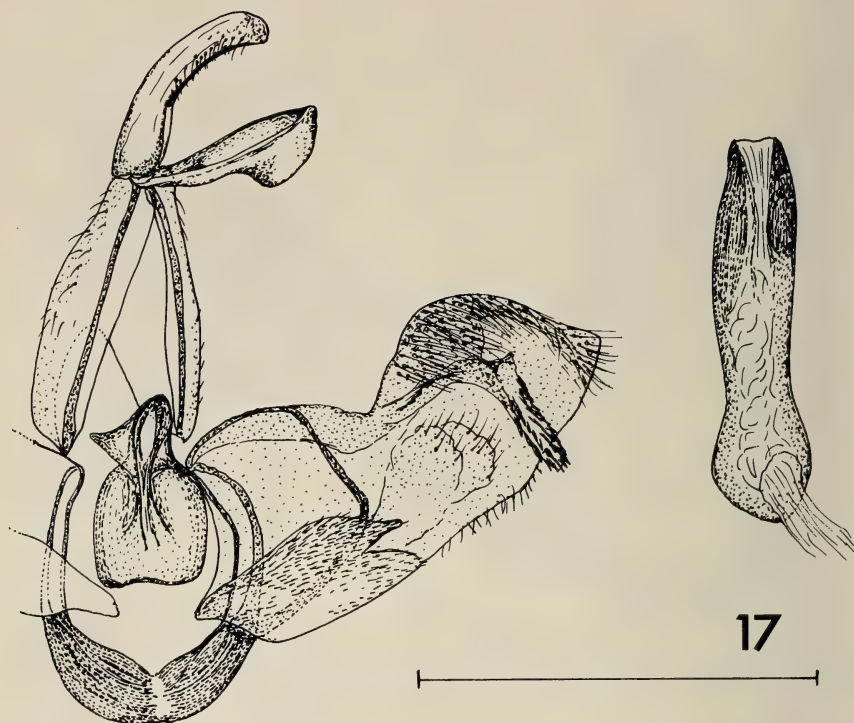
FIG. 12. Male genitalia of *Neoeromene parvalis*, posterior aspect with left valva (left), aedeagus (right). Scale = 1 mm.

spur at about 0.4; valva crossed by narrow membranous zone from base of this spur obliquely to base of costal margin. Aedeagus tubular, LMB ratio about 8:1, curved gently ventrad, apex bearing pair of broad curved spurs, one larger than the other.

Female genitalia (Fig. 11) (N = 1). Anal papillae broad, prominent, moderately fused dorsally; 8th abdominal tergum narrow, barely as long as anal papillae; anterior and posterior apophyses approximately equal in length; posterior margin of 7th sternum medially indented, infolded. Antrum a broad, globate, sclerotized funnel, basally constricted at about 0.2; ductus bursae complexly folded, with 2 or more small, membranous, lateral, subantral pockets; position of ductus seminalis junction difficult to determine in preparation, apparently at about 0.5; corpus bursae asignate, massive.

Types. Holotype *parvalis* ♂, BRAZIL: "Ega (Brazil) 57-125", BMNH, genitalia prep. BM pyral 7679.

Holotype *excitata* ♀, BRAZIL: Obidos, VIII.19, Parish, BMNH genitalia prep. BM pyral 7681.

Other material examined. PERU: 4 ♂, Iquitos, VIII.1920, Cornell Univ. Exp. Lot 607, MCU, genitalia prep. Cornell #1 (M. Shaffer); 1 ♂, 1.VIII.1920 (same Cornell lot. no.), CNC, genitalia prep. 4382-SB.

Discussion. The genitalia of both sexes demonstrate clearly the major characteristics of this genus; the male uncus is apically divided, and the sacculus of the valva strongly developed, while in the female the broad antrum is sclerotized, the subantral region of the ductus is complex, and the corpus bursae asignate. Nothing is known of the geo-
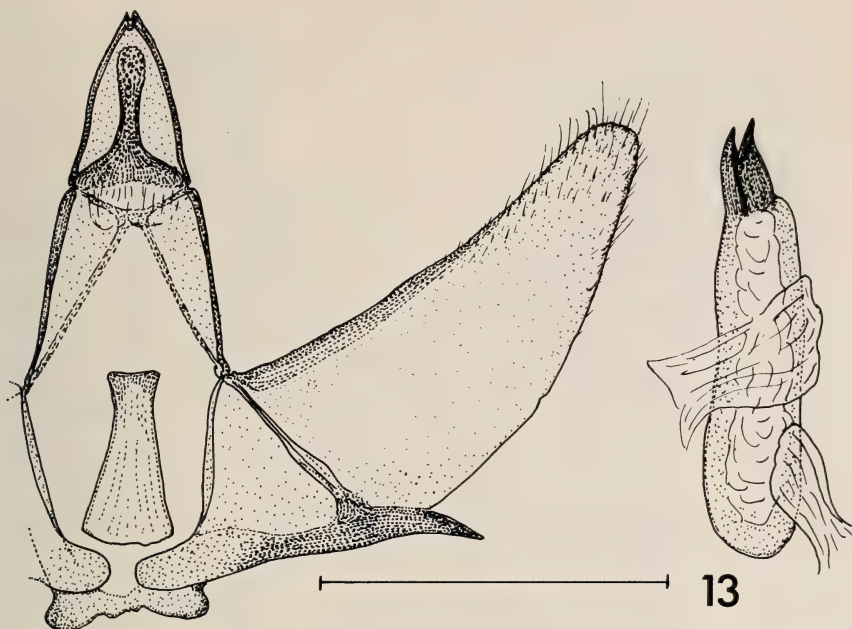
FIG. 13. Male genitalia of *Neoeromene herstanella* holotype, posterior aspect with left valva (left), aedeagus (right). Scale = 1 mm.

graphic distribution and ecology, except that it appears to occur across the upper Amazon region and the flight period includes August.

Neoeromene herstanella (Schaus), new combination

Diptychophora herstanella Schaus (1922:132).
Diptychophora herstanella Schaus; Błeszyński & Collins (1962:297).
Pareromene herstanella (Schaus) Błeszyński (1967:92, 96).

Description. Alar expanse 9 mm (Fig. 3) (N = 2). External features adequately described by Schaus (1922).

Male genitalia (Fig. 13) (N = 1). Uncus broad, tapered, bluntly pointed; apex minutely cleft. Gnathos slender, tubular, distal half rugose or "pimpled". Tegumen simple, broad, strong; vinculum triangular in profile, about half as wide as uncus length; saccus small, truncate, with angles slightly pointed; juxta an elongate plate, broad at base, otherwise narrow, weak; membranous anellar structure present. Valva 4.0–4.2× length of uncus; costal region a sclerotized strip running dorsal length of valva, without prongs or protrusions; valvula tapered to blunt dorsal point; sacculus with distinct lobe, drawn distally into a prong directed posterioventrad, 0.5× length of uncus. Aedeagus about 0.7× length of valva, stout. LMB ratio about 5.5:1, with pair of large, recurved apical horns; cornuti absent.

Female genitalia (Fig. 15) (N = 1). Anterior and posterior apophyses approximately equal in length; anal papillae separate. Antrum a sclerotized tapered funnel, with basal swellings; ductus bursae about 4.5× length of posterior apophyses, slender; ductus seminalis joining at about 0.4; corpus bursae relatively small and asignate.
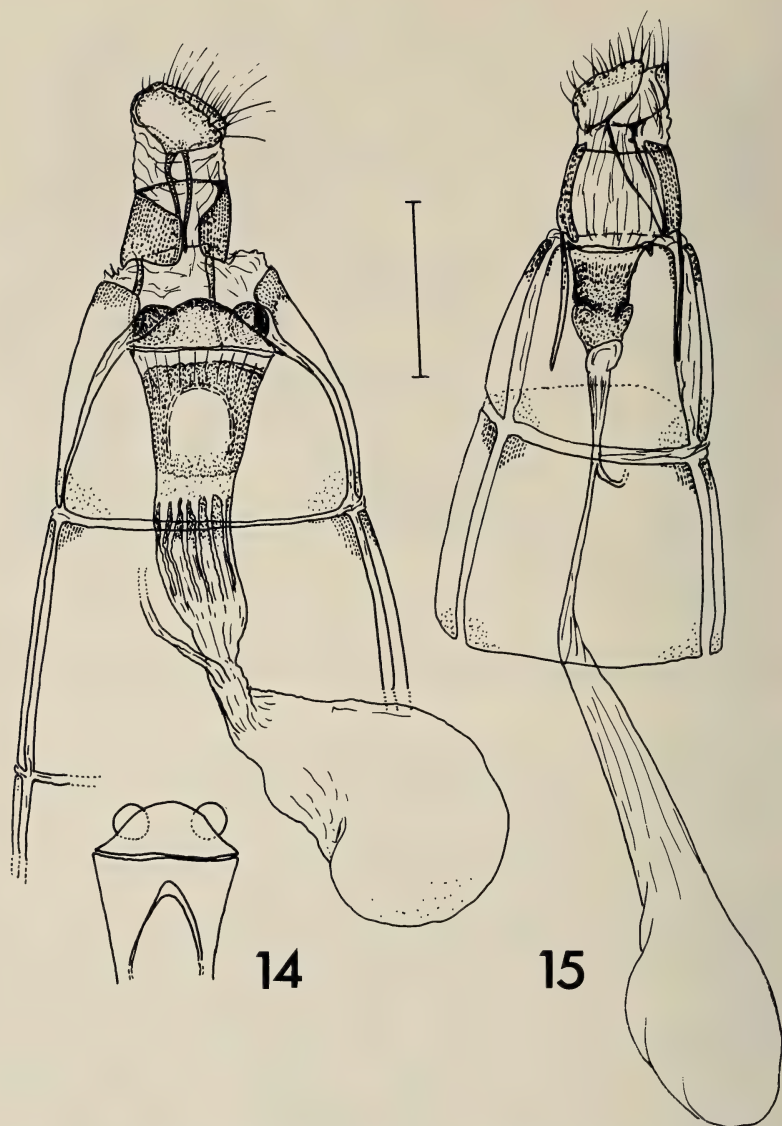
FIGS. 14, 15.   **14,** Female genitalia of *Neoeromene felix* (*leucanthes* holotype); **15,** *N. herstanella*; both ventral aspect. Scale = 1 mm.

Types. Holotype ♂, PANAMA: with 4 labels; "Porto Bello, Feb. 24. Pan." (white), "Type No. 25535 U.S.N.M." (orange), "slide SB ♂ No. 4617" (pale blue), "*Diptychophora herstanella* type. Schs." (white).
    Other material examined. 1 ♀, COSTA RICA: Siguirres, Limon, 50 m, no date. BM 16753.
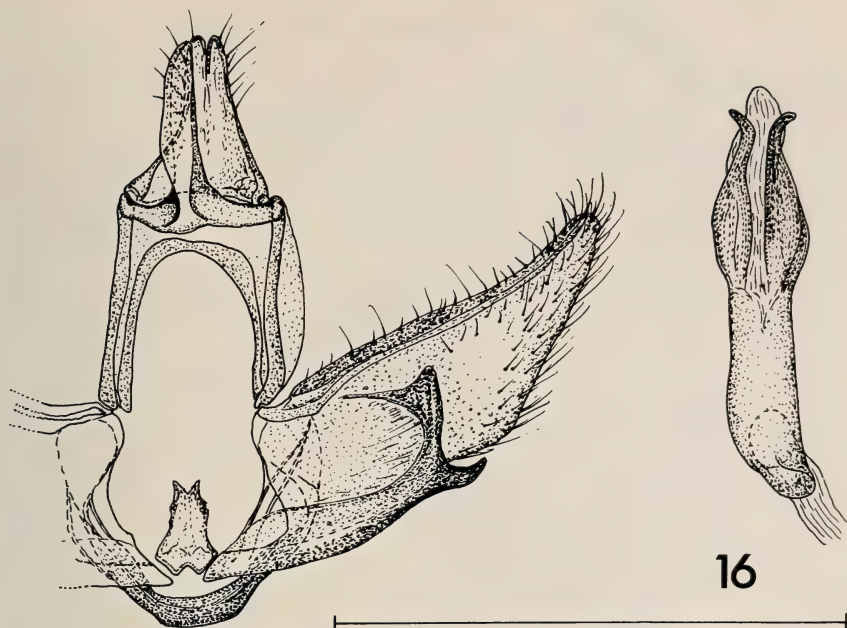
FIG. 16. Male genitalia of *Neoeromene octavianella*, paralectotype, posterior aspect with left valva (left), aedeagus (right). Scale = 1 mm.

Discussion. This species is presently known only from Panama and Costa Rica, with a flight period including February. It is close to *parvalis* in major genitalic characters, and may be a Pleistocene segregate from that species.

Neoeromene octavianella (Zeller), new combination

Diptychophora octavianella Zeller (1877:33, pl. 1, fig. 13).
Diptychophora octavianella Zeller; Błeszyński & Collins (1962:298).
Pareromene octavianella (Zeller) Błeszyński (1967:92, 96).

Description. Alar span 12–14 mm (Fig. 2) (N = 3). Described here because Zeller's account does not fully distinguish it from similar species. Female not yet collected. Head, thorax, palpi dull whitish with some grey and buff. Ground color of forewings off-white. Basal fascia represented by some blackish brown scales. Antemedial fascia more distinct, dull brown, slightly zigzagged. Faint yellow reniform mark present in disc, which has scattered buff scaling. Postmedial fascia a broad creamy band, zigzagged near apical angle and towards dorsum, edged thinly with dark brown. Terminal zone white, with 2–3 small blackish spots on margin between 0.5–0.8, surrounded by some yellow scales. Apical zone bright yellow, with suboval, central, shining white patch not touching costa. Small wedge of white scales present at apical extremity. Hindwings whitish. Cilia pale brown with darker tips. All ventral surfaces dull mid-brown, with apical and terminal markings repeated from dorsal surface.
Male genitalia (Fig. 16) (N = 2). Uncus broad, slightly setulose, tapered, with bifid apex. Gnathos slightly shorter than uncus, T-shaped, with strong base nearly at right angles to subapically swollen perpendicular element. Tegumen simple, with thick, strong

FIG. 17. Male genitalia of *Neoeromene parvipuncta*, holotype, posterior aspect with left valva (left), aedeagus (right). Scale = 1 mm.

dorsal and ventral margins; vinculum indistinguishable from saccular lobe of valva; saccus short, broad, straplike and posteriorly truncate; juxta subtriangular, apically tapered, indented basally and developed apically into pair of short prongs. Valva nearly 3× uncus length, costal margin strong to the tapered apex; sacculus-vincular region developed into a distinct lobe, ventral margin strong, with zone of sclerotization running introrse into central part of valva, almost touching base of costa, thick, short, curved thorn at 0.5. Aedeagus about 0.8× length of valva, stout, LMB ratio about 7:1, lacking cornuti, with apical portion divided to form pair of strong, apically recurved prongs lateral to ductus ejaculatorius.

Types. Lectotype ♂ (here designated), PANAMA: "Chiriqui Ribbe", Coll. Staudinger, "*Diptychophora octavianella*" [blue label]; "Origin" [pink label]; "Typus" [red label]; "Praep. Gen. Nr670♂" [Błeszyński]; "D2.845 Lectotype" [circular purple-bordered label]; "LECTOTYPE *Diptychophora octavianella* Zeller det. M. Shaffer. 1976", MNHU.

Paralectotypes, 2 ♂, data as above except one has basic data on white (not blue) label, both bear "Paralectotype" [circular blue-bordered labels]; one bears "Abdomen missing" [blue label]; both bear "PARALECTOTYPE *Diptychophora octavianella* Zeller det. M. Shaffer. 1976" [white labels]; one bears "73?" [faded paper], MNHU.

Discussion. *Neoeromene octavianella*, presently known only from Panama, forms part of a closely related cluster of species including *N. parvalis* and *N. herstanella*.

Neoeromene parvipuncta, new species

Description. Alar span 11 mm (Fig. 5) (N = 1). Labial palpi 1.2× head length, yellowish, with blackish tips. Head, thorax and abdomen yellowish with occasional patches of paler cream and dark brown scales. Tarsi of forelegs banded alternately with buff and dark brown. Ground color of forewings golden yellow; basal fascia obsolete, marked only by a few irregular patches of blackish brown; antemedial fascia dark brown, irregular, incomplete, narrow. Discal region of forewing overlain with pale cream scaling; central area with some black or brown patches, but no distinct reniform stigma. Postmedial fascia white, distinct, broad, sharply edged with dark brown. Some fine dark neural streaks extend from disc to termen. Apical region orange, with a central pear-shaped white zone, edged posteriorly with dark brown, some dark brown shading on costa. Terminal region golden yellow, subapical marginal indentation distinct; termen bearing 5–6 indistinct blackish spots set in small areas of white scales, from 0.3 to 0.9. Hindwings white, clouded near apex with pale brown. All cilia pale brown with dark brown tips.

Male genitalia (Fig. 17) (N = 1). Uncus curved, bluntly tapered, laterally setulose. Gnathos slightly longer than uncus, apically swollen and cupped. Tegumen with strong posterior margins; saccus simple, broad, apically rounded; vinculum broad, almost as wide in profile as uncus length; juxta broad, quadrate, drawn into pair of anellarlike dorsal projections which close around aedeagus. Valva about 2.2× length of uncus, bluntly tapered; costal region strong, terminating in a heavily spinose protrusion arising at 0.5–0.6 and curving introrse, posteriad, then ventrad inside valva. Valva with slight dorsoventral constriction at about 0.5; sacculus a spinose lobe partially segregated from base of valvula. Aedeagus about 0.8× length of valva, tubular, straight, truncate, with dorsal and ventral zones of apical-subapical sclerotization, not drawn out into apical prongs; LMB ratio about 5.5–6.0:1; cornuti absent.

Type. Holotype ♂, BRAZIL: Curitiba, Parana, 920 m, –.X.1975, V. O. Becker, in V. O. Becker collection, specimen 4823.

Discussion. Nothing is known of the biology of this species; the type specimen was taken in October. On genitalic characters it is closely related to *N. straminella*.

Neoeromene straminella (Zeller), new combination

Diptychophora straminella Zeller (1877:32, pl. I, fig. 12).
Diptychophora straminiella Zeller; Hampson (1896 (1895):943) (misspelling of *straminella*).
Diptychophora straminella Zeller; Błeszyński & Collins (1962:299).
Pareromene straminella (Zeller) Błeszyński (1967:92, 96).

Description. Alar span 14–15 mm (Fig. 6) (N = 3). Redescribed here; there is more variation than indicated by Zeller. Female not yet collected. Labial palpi about 0.75× head length, yellow, with blackish apices and transverse striping. Head, thorax, abdomen creamy yellow with sprinkling of chocolate scales. Ground color of forewings pale yellowish orange, basal fascia nearly obsolete. Double, faint, reniform stigma present, together with some faint interneural streaks in discal region. Postmedial fascia creamy yellow, thinly edged with dark brown. Terminal zone yellowish, clouded with dark brown, except distally, where the margin bears a row of 5 black spots set in a narrow strip of orange-ochreous. Apical zone bright orange-brown, with a central triangular white mark, banded thinly with black proximally and posteriorly. White wedge of scales at apical costal extremity. Cilia pale brown with darker apices. Ventral surfaces straw, with some repetition of dorsal apical and terminal markings.

Male genitalia (Fig. 18) (N = 2). Uncus narrow, tapered, bluntly pointed, curved ventrad. Gnathos subtubular, swollen abruptly at 0.5, then tapering to bluntly pointed apex, curved dorsad. Tegumen simple, with strong ventral margins. Vinculum broad, about 0.75× as wide as uncus length. Saccus large, broad, rounded, about as long as
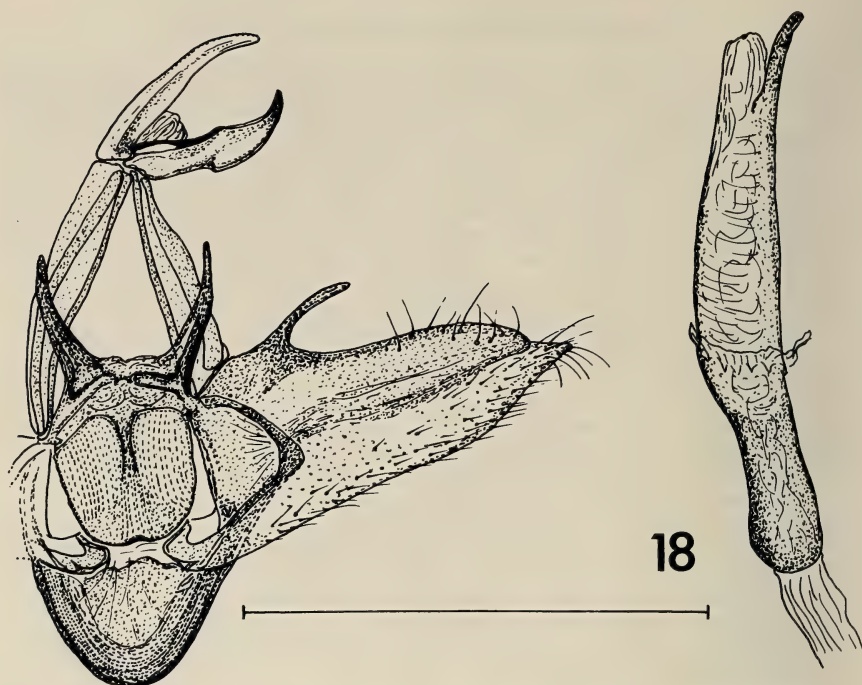
FIG. 18. Male genitalia of *Neoeromene straminella*, posterior aspect with left valva (left), aedeagus (right). Scale = 1 mm.

uncus. Juxta an apicomedially cleft quadrate plate, more rounded basally than apically, fused with an anellar structure bearing a pair of large, curved, strong apical horns, bases of which are partially fused laterally with basal extremities of valval costa. Valva about 2.5× length of uncus, sacculus weakly developed, costa strong, bearing a curved basal prong nearly half uncus length; costal lobe extends almost to apex of valva, apex discrete and partly separate. Aedeagus about 1.4× length of valva, curved slightly dorsad, LMB ratio about 8:1. Cornuti absent, but apex bears an elongate, blunt thorn dorsally.

Type. Holotype ♂, BRAZIL: "N. Friburgo Bres.", *Staudinger* (also bears labels "Origin", "Typus", "7:?"), MNHU, genitalia prep. GS-603-SB.

Other material examined. 2 ♂, BRAZIL: Petropolis, *Walsingham*, BMNH, BM pyral 15093.

Discussion. So far collected only in Brazil, a close relative of *herstanella* and *parvalis*. Flight period unknown.

Neoeromene felix (Meyrick), new combination

Diptychophora felix Meyrick (1931:108).
Diptychophora leucanthes Meyrick (1931:108); Błeszyński & Collins (1962:297). **NEW SYNONYMY.**
Diptychophora felix Meyrick; Błeszyński & Collins (1962:297).
Pareromene felix (Meyrick) Błeszyński (1967:96).
Pareromene leucanthes (Meyrick) Błeszyński (1967:92, 96).
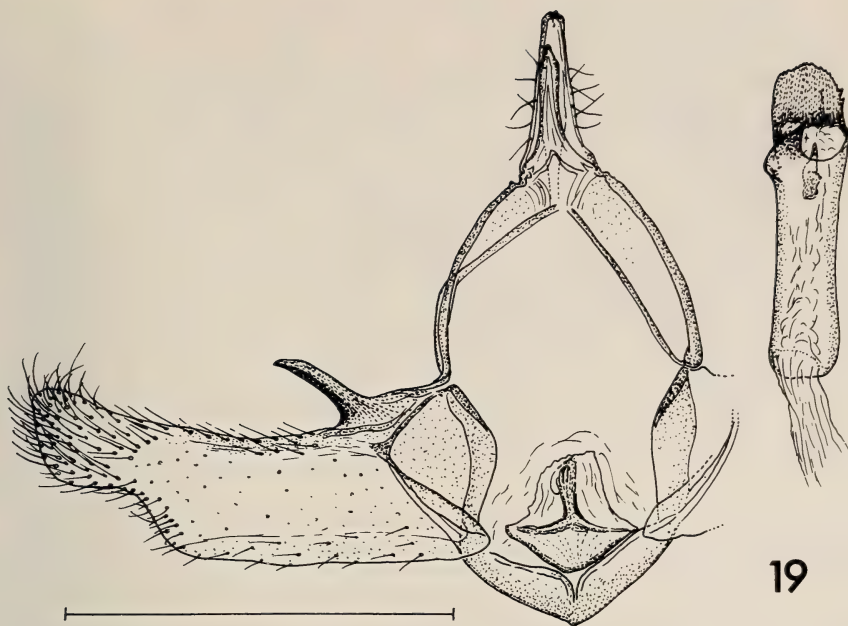
FIG. 19. Male genitalia of *Neoeromene felix,* lectotype, posterior aspect of left valva (left), aedeagus (right). Scale = 1 mm.

Description. Alar span 12–13 mm (Fig. 7) (N = 10). External features adequately described (twice) by Meyrick (1931). Characters described for *leucanthes* overlap those for *felix*.

Male genitalia (Fig. 19) (N = 2). Uncus simple, tapered, lightly setulose, curved ventrad, with blunt apex. Gnathos about 0.8× uncus length, curved slightly dorsad, tapered abruptly near base, then parallel-sided until near slightly hooked, pointed apex. Tegumen simple; vinculum broadly triangular, about 0.7× as wide as uncus length; saccus broadly pyramidal, about 0.5× uncus length; juxta a subtriangular plate, with a sclerotized inverted "Y" strengthening dorsal apex and expanded ventrolateral margins. Valva broad, sacculus barely differentiated, costal region strong to about 0.5, with thick, simple, slightly curved basal prong 0.7× uncus length. Valva parallel-sided to about 0.7 from base, then tapering abruptly to a quadrate, setulose, apical lobe. Aedeagus about 0.7× valval length, tubular, truncate, stout, LMB ratio about 6.5:1, apex bearing a broad, flattened, spade-shaped, strongly sclerotized spur with serrate margin, and a second much smaller hooked spur below exit of ductus ejaculatorius. A single large, irregular cornutus present subapically.

Female genitalia (Fig. 14) (N = 2). Anal papillae moderately fused, anterior and posterior apophyses nearly equal; 8th tergum about 0.8 × length of posterior apophyses; 7th sternum rounded and partly tapered posteriorly; sternum margin turned introrse, combining with lamella antevaginalis into a lodicular structure while lamella turns extrorse, forming a protruding lip. Lateral extremities form a pair of nearly circular cuplike structures directed ventrad. Lamella postvaginalis set deep in the broad antrum, medially broadly fenestrate. Ductus bursae about 3.5× length of posterior apophyses, with ductus seminalis joining at about 0.9, close to corpus bursae; ductus bursae pleated from 0.4–0.6; corpus bursae asignate.
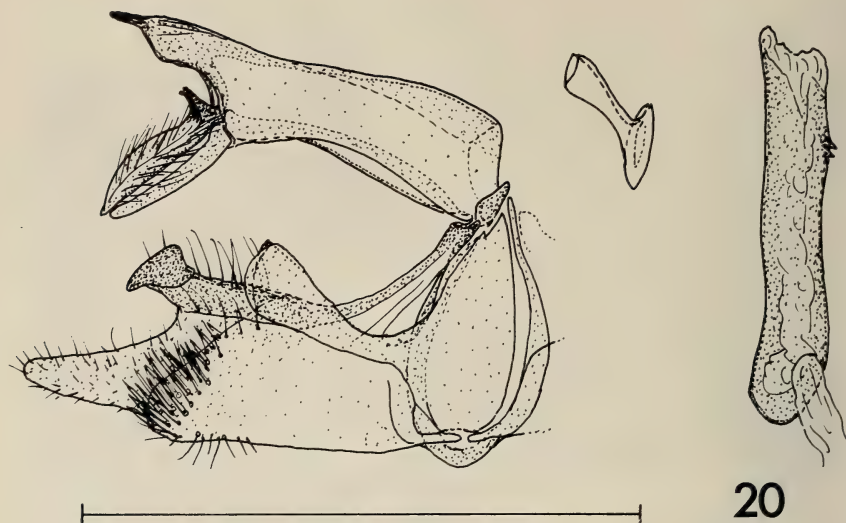
FIG. 20. Male genitalia of *Incaeromene subuncusella*, holotype, posterior aspect with left valva (left), aedeagus (right). Scale = 1 mm.

Types. *N. felix:* Lectotype ♂ (selected by S. Błeszyński and designated here). BRAZIL: Obidos, "8.19", Parish BMNH, genitalia pre. BM pyral 7682.

Paralectotypes, BRAZIL: 4 ♂, one lacking abdomen, data as above but "8 & 9.19", BMNH; 1 ♀, data as above, BMNH, and bearing label in Błeszyński's writing "BM ♀ 7684", but unfortunately the slide is missing from the collection; 1 ♂, Santarem, "8.19" Parish, BMNH, BM pyral 7683.

N. leucanthes: Holotype ♀, PERU: Iquitos "3.20", Parish, BMNH, genitalia prep. BM pyral. 7682.

Other material examined. GUYANA: 1 ? (lacks hindwings, frenula, abdomen): Confluence of Orinoque & New Rivers, 20.viii–20.ix.1937, Hudson, BMNH; ?BOLIVIA: 1 ♀, "Carn. Mus. Acc. 6473" (no other data), CM, genitalia prep. GS-5983-SB.

Discussion. Variation in the proportions of brown and yellow clouding in different specimens is considerable. Based on his criteria for distinguishing species, Meyrick's (1931) conclusions were reasonable. This species is probably widespread in the tropical forests of the northern and central regions of South America. The flight period is known to include August and September.

Incaeromene, new genus

Type species *Incaeromene subuncusella*, new species (original designation).

Description. Venation as in *Neoeromene*. Genitalia characterized by singular development of dorsal region of tegumen into a hood, projecting over uncus and gnathos, terminating in a strong spur posteriad, also by costal lobe of valva bearing a broad capitulate protrusion. Sacculus strongly developed as in *Neoeromene*, but posteriorly heavily spinose on inner surface.

Etymology. Inca—pertaining to Incas; Ερωμένη (Eromenē)—mistress (f).

Incaeromene subuncusella, new species

Description. Alar span 15 mm (Fig. 8) (N = 4). Head, labial palpi, thorax, abdomen silvery white; medial surfaces of palpi and patagia with scattered chocolate-brown scaling. Ground color of forewings silvery white. Basal and antemedial fascia obsolete, positions marked by some brown scaling. Postmedial fascia composed of pair of curved brown lines. Termen with weak subapical indentation at about 0.25, and 3–4 black marginal spots from 0.5–0.9. Faint reniform mark present in disc amid patch of brown scaling, some similar clouding on costa at base and subterminal region. Cilia white with brown bars. Hindwings pure silvery white, as are cilia. Underside of forewings dull brown.

Male genitalia (Fig. 20) (N = 1). Uncus and gnathos stout, tapered, pointed, slightly curved, setulose. Uncus with pair of sclerotized basal dorsal protrusions. Tegumen strong, drawn dorsoposteriorly into long hood over uncus, terminating in sharp, sclerotized point. Saccus negligible, vinculum narrow. Juxta weak, laterally folded and posteriorly drawn into an anellar structure around aedeagus. Valva about 2.7× uncus length, with broad sacculus, lobate posteriorly, heavily spinose. Costal region drawn into broad, bluntly capitulate setulose lobe. Aedeagus 2.2× uncus length, massive, apically lightly sclerotized, with pair of small dorsal subapical thorns.

Type. Holotype ♂, PERU: Cuzco, Pillahuata, 2600 m, 14–18.viii.1982, M. Matthews & M. Packer. BMNH genitalia prep. pyral. 17131, in BMNH. Paratypes 3 ♂, same data as holotype, all in BMNH.

Discussion. This undistinguished looking species exhibits the most peculiar modification of the dorsal tegumen of any known diptychophorine. Without female genitalia, it is impossible to speculate about the function of this spurred hood over the uncus.

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BOOK REVIEW

Butterflies East of the Great Plains, by Paul A. Opler and George O. Krizek. 1984. The Johns Hopkins University Press, 701 West 40th Street, Suite 278, Baltimore, Maryland 21211. Pp. 17 + 294. Price: $49.50 + shipping.

The book gives comprehensive accounts of the butterflies of the thirty-one states east of the Great Plains. Detailed descriptions of more than 250 species are clearly and succinctly presented. The illustrative material, including detailed maps and 324 spectacular color photographs obtained in the field, add much to the species accounts. Some readers will no doubt complain that the 54 colored plates are set off in the central part of the book and not included with the species descriptions, but the very beauty of the photos as well as their taxonomic utility is best served by having them together.

In the species accounts, the authors present the etymological derivation of the scientific name and a synopsis of the species, stating any noteworthy trait. A lengthier discussion and description of the butterfly follows, which includes its distinguishing characteristics, geographic variation, and various meaningful attributes including statistical measurements of both sexes. Both descriptive and map forms are used to present the overall range. Where applicable, they indicate temporary expansion of range beyond where the species is normally resident. A surprising number of species are indicated whose temporary northern extension of range is cut back by the severity of winter. The extensive review of county records contributed by more than one hundred lepidopterists helps make the data on distribution and habitat one of the most valuable contributions of the book. Habitat descriptions are provided for each species including specific vegetation, plant formations, and even associated soil types.

The format for the species accounts also includes sections on life history and food sources, involving adult nectaring data as well as caterpillar host plants, and it is in these details that Opler and Krizek shine. The sections are full of data and challenging observations which ought to provoke much more interest and enthusiasm among readers in adding to natural history observations.

A lucidly written 33-page introduction contains a series of short essays on smaller topics reflecting the interests of field naturalists. Here the authors discuss such things as patterns of diversity, seasonality, and distribution. These sections should also whet the intellectual appetite and leave readers anxious to learn more.

I find this book very revealing and exciting and feel it will be a valuable addition to the library of every lepidopterist, including those of "professional" as well as "amateur" standing. Part of its beauty lies in the obvious knowledge of field natural history possessed by the authors. It is well done! I hope they will favor us with another volume or two on the natural history of butterflies.

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BIOLOGY AND DESCRIPTION OF IMMATURE STAGES OF *PHIGALIA STRIGATERIA* (MINOT) (GEOMETRIDAE)

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ABSTRACT. Egg, larva, and pupa of *Phigalia strigateria* (Minot) are described for the first time from a population in eastern West Virginia. Eggs were deposited under loose bark of dead twigs. Thirty-two species of trees and shrubs were observed as larval hosts, with preference being shown for oaks, hickories, and common hackberry. Five larval instars and seven larval color forms were noted. Mean developmental time from egg to pupa was 28 days at 24°C.

Four species of North American *Phigalia* belonging to the holarctic tribe Bistonini have been described (Rindge 1975). Three of the species, *P. titea* (Cramer), *P. denticulata* Hulst, and *P. strigateria* (Minot), are found only in eastern North America. Immature stages have been described only for *P. titea* (Butler 1985a, Talerico 1968).

The distribution of *P. strigateria* was given by Rindge (1975) as eastern North America, southern Ontario, and Quebec, from the Atlantic Ocean to about longitude 100°W. While adult *P. strigateria* have been often recorded, almost no information is available on immature stages. Prentice (1963) reported a single larval collection from *Ulmus americana* L. at Brockville, Ontario, in June 1950; he considered the species rare in that locality.

Beginning in 1981, significant defoliation of hardwood forests in eastern West Virginia was attributed to a looper complex. Some larval collections were made in 1982, and a detailed study of the looper complex was conducted in 1983 and 1984. *Phigalia strigateria* was sufficiently abundant to provide material for biological and descriptive studies. Results of these studies are presented here.

MATERIALS AND METHODS

Study areas were in eastern West Virginia in an oak-hickory-pine forest on dry upland sites. Two study areas were on Cacapon Mountain (Cacapon State Park) in Morgan Co. One area, Batt Picnic Area (Batt), was at 381 m elevation, while the Cacapon Overlook area (Cac) was at 701 m. The Elkhorn Mountain (Elk) area was on the border of Grant and Hardy counties at 732 m elevation. During 1981–82, Batt was 100% defoliated while the other sites were about 25% defoliated. Defoliation in 1983 was greatly reduced because populations collapsed, and by 1984 defoliation was sparse.

Field studies were begun with observations and collections of emerging adult *P. strigateria* on 17 March 1983. Samples of adults were

taken for species confirmation and collection of eggs. Oviposition habits were noted and fecundity was determined by allowing field-collected females to oviposit on dead twigs in the laboratory. All laboratory studies were conducted at 24°C and 12:12 photoperiod. Moths were not provided with food or water as the mouthparts are rudimentary.

Larvae were collected in the field and their host plants recorded. Botanical nomenclature is that of Bailey and Bailey (1976). Stage durations were determined by rearing 60 larvae hatched from eggs laid in laboratory cages. Larvae were reared on leaves of sugar maple in groups of 10 in large Petri dishes. Larvae were checked daily and food was changed every other day. Descriptions were based on both laboratory-reared and field-collected larvae and pupae. Terminology follows Hinton (1946) and McGuffin (1967). Larval head measurements were made with an ocular micrometer; early instars were measured at 30× and later instars at 10×. Illustrations of larvae and pupae are by the author. Voucher specimens of larvae and adults are in the West Virginia University Collection.

RESULTS

Phenology, Life History, Food Plants

In all study areas, the seasonal occurrence of *P. strigateria* was similar to that of *P. titea* (Butler 1985b). Adults were collected at Batt on 17 March 1983 and at the higher altitudes of Cac and Elk beginning 24 March. Males were most often observed resting on tree trunks, while females were climbing tree trunks, resting, or ovipositing on dead twigs. Female *Phigalia* taken at the study sites between 31 March and 26 April were primarily *P. titea*. Females of *P. strigateria* made up the following percentage at each site: Batt 9% (21n), Cac 10% (29n), Elk 8% (26n).

Oviposition habits of *P. strigateria* are similar to those of *P. titea*; eggs are deposited most frequently under loose bark or in cracks or roughened areas of dead hardwood twigs. Females were observed ovipositing in the field on dead twigs of *Acer* spp., *Cornus florida* L., *Quercus* spp., *Betula lenta* L. and *Hamamelis virginiana* L. Field-collected females (9n) lived two to four days in the laboratory and began ovipositing one to two days after being brought from the field. They oviposited a mean of 149 (range 26–319) eggs (9n). Females producing the fewest eggs had probably begun ovipositing before they were collected.

Five larval instars were found for this species; mean developmental time from egg to pupa was approximately 28 days at 24°C (Table 1).

Field larval development was similar to that of *P. titea* (Butler 1985a).

TABLE 1. Development time of *P. strigateria* reared on leaves of sugar maple at 24°C. Means based on 60 larvae.

Instar	Time in instar (days)	
	Mean	Range
1	4.1	3–5
2	3.4	2–4
3	3.4	2–5
4	3.2	2–4
5	7.2	6–9
Prepupa	6.5	5–9
Total	27.8	21–34

Egg hatch in 1983 began about 1 May at the lower altitude at Batt and about a week later at the higher altitudes. Larvae hung down on silk lines and ballooned away from dead twigs on which they hatched. Larvae fed for four to five weeks at each site before they moved into the soil to pupate.

Larval populations at all three study sites in 1983 consisted largely of *P. titea*, ranging from 77 to 94% (2,162n) of the population at Cac and Elk, respectively. Larval percentages of *P. strigateria* at the study sites were: Batt, 4%; Cac, 8%; and Elk, 3%. Other species of larvae present in noticeable numbers were linden looper, *Erannis tiliaria* (Harris), 2–13%; and fall cankerworm, *Alsophila pometaria* (Harris), 1–2%.

Phigalia strigateria larvae were observed feeding on the following 32 hosts:

Juglans nigra L.
Carya ovata (Mill.)
C. tomentosa Nutt.
C. glabra (Mill.)
Betula lenta L.
Corylus americana Marsh.
Quercus alba L.
Q. prinus L.
Q. stellata Wangenh.
Q. rubra L.
Q. coccinea Muenchh.
Q. velutina Lam.
Ulmus rubra Muhlenb.
Celtis occidentalis L.
Hamamelis virginiana L.
Crataegus spp.

Amelanchier canadensis (L.)
A. ×grandiflora Rehd.
Malus sylvestris Mill.
M. coronaria (L.) Mill.
Rubus spp.
Prunus serotina Ehrh.
Cercis canadensis L.
Acer negundo L.
A. saccharum Marsh.
A. rubrum L.
A. pensylvanicum L.
Tilia americana L.
Parthenocissus quinquefolia (L.) Planch.
Nyssa sylvatica Marsh.
Cornus florida L.
Vaccinium augustifolium Ait.

Host plants of *P. strigateria* are similar to those of *P. titea* (Butler 1985b).

Favored host plants appeared to be oaks, hickories, and hackberry. Only on hackberry was the percentage of *P. strigateria* larvae within the looper population markedly different from that previously mentioned; *P. strigateria* larvae appeared to make up 40–70% of the looper population on hackberry observed at Batt and Elk.

During 1983, high rates of parasitism by tachinids, ichneumonids, and braconids were observed in field-collected larvae of all four geometrid species. Parasitism was highest for *P. strigateria*, however, reaching 70–90% (135n) in some larval collections. While populations of all looper species in the study areas showed a dramatic collapse in 1983, the collapse of *P. strigateria* was especially notable. In 1984, no adult *P. strigateria* were found, and larvae made up less than 0.01% (250n) of the population at each site.

Description of Immature Stages

Eggs. Eggs are sculptured, slightly rough textured, and oblong, with one end broadly rounded or blunt and the other end conical. They are yellow, becoming duller just before hatching. Empty *P. strigateria* chorions are a pale golden yellow in contrast to those of *P. titea* which are pale lavender. Eggs laid in the laboratory by field-collected females had a mean length of 0.75 mm (range 0.66–0.79) and mean width of 0.45 mm (range 0.40–0.50) (80n).

Larvae. Instars 1 through 3 are uniform in color. Larvae of the last two instars show much variability. The following descriptions are of coloration and mean head widths of instars of the most abundant color form of *P. strigateria*.

Instar 1 (26n): Head (0.27 mm) pale yellow-brown; ground color of body pale greenish tan; pinnaculae black surrounded by white cuticle. Broad diffuse dorsal stripes and broad irregular lateral stripes are greenish white. Cervical shield pale brown; lateral shields of anal prolegs brown, prominent.

Instar 2 (8n): Head (0.50 mm) pale yellow-brown with reddish brown granulations. Ground color of body dark greenish black. Pinnaculae not prominent; setae near spiracles each on a small white chalaza. Dorsal stripes greenish white, prominent when viewed with magnification, but very fine, irregular, and broken. Greenish white subdorsal and lateral stripes just above and below spiracle with diffuse grayish white fill around spiracle. Lateral stripe most prominent on abdominal segments 1–6. Ventral proleg greenish black. Anal plate grayish white with greenish black maculations; anal proleg shields prominent, color of ground, contrasting with paler color of anal segment. Mid-ventral pale stripe expanded at middle of each sternite. Secondary setae are present for the first time in this instar.

Instar 3 (33n): Similar to instar 2. Head (0.81 mm) reddish brown. Dorsal and lateral stripes more prominent. Lateral stripe yellowish, extending down ventral proleg; absent beyond sixth abdominal segment. Anal plate and prolegs pale tan with brownish maculations.

Instar 4 (25n): Head capsule (1.36 mm) yellow, roughened with reddish brown maculations; thoracic legs reddish brown; body ground color black. Dorsal stripes yellow, fine, irregular, often not continuous; black fill frequently between stripes but not consistent; stripes most prominent on abdominal segments 1–2 and 6–9. Dorsal chalazae of eighth abdominal segment most prominent. Lateral stripe irregular, yellow, generally broad and most prominent on abdominal segments 1–6, weak on thorax; on abdominal segment 6, stripe extends down proleg and terminates; lateral striping on posterior abdominal segments appearing only as yellow flecks. Spiracles with black peritreme; spiracular valve yellow. Cervical shield black with brownish tan irregular fill. Anal and

TABLE 2.   Percentage of color forms of 4th and 5th instar *P. strigateria* collected between 17 May and 8 June 1983.

Study site	No. larvae	Percentages						
		Typical	Dark	Pale	Yellow/ stripe	Yellow	Orange	Brown
Batt	97	69	1	16	11	2	0	1
Cac	139	35	5	19	26	7	6	2
Elk	60	40	0	19	18	5	18	0

proleg shields prominently mottled yellow-brown. Venter yellowish brown with pale yellow mid-ventral stripe.

Instar 5 (34n): Head capsule (2.24 mm) as in instar 4. Legs tan and dark brown. Dorsal stripes well developed on first nine abdominal segments, partially developed on metathorax, as dashes only on mesothorax, absent on prothorax; stripes yellow, often giving a chain-link appearance dorsally. Cervical shield and anal prolegs granulate dull brown; anal plate pale tan with small, dark maculations. Venter with a broad tan stripe expanded on each segment; stripe on abdominal sternites 7–8 often paler. Other features similar to those of 4th instar.

The most frequently observed variations in color patterns of instars 4 and 5 were the pale form and yellow form with subdorsal stripe.

Pale form—Yellow striping more intense. Dorsal stripes broad, pale yellow with middorsal dark dashes only on thorax; only a narrow band of black above the broad yellow lateral stripe. Dashed black subventral line; legs brown with dark coxae. Cervical and anal shields yellow with brown maculations.

Yellow form with subdorsal stripe—Head paler than on darker forms. Ground color of body yellow. Dark points include only a prominent black subdorsal stripe which is continuous from prothorax through abdominal segment 10 or continuous only to abdominal segment 5, and chalazae on abdominal segments 2, 3, and 8, which are often black.

Other variations included a yellow form without subdorsal stripes; an orange form, similar to the typical form but with orange replacing yellow; a dark form with all pale patterns reduced; and a brown form.

Samples of 4th and 5th instar *P. strigateria* collected at the study sites from 17 May through 8 June consisted of the forms in Table 2.

Chaetotaxy of last instar: Head with P1 somewhat in front of P2; A2 in front of and below A3 and above A1; L1 directly above 02; 01 directly posterior to ocellus 3; AF1 and AF2 widely separated; F1 almost directly below AF1 and above and in front of C2; C1 close to C2 and on edge of adfrons; labrum with L2 and M2 longer than other labral setae; 02 and C1 longest of all head setae (Figs. 1, 2). Prothorax with XD1, XD2, D1, D2 and SD2 approximately equidistant from each other; SD1 very small and close to SD2; L2 small and directly below L1: SV1 longer than SV2 (Fig. 8). On mesothorax D1, SD2 and L3 in a vertical line; D2 and SD1 anterior; SD1 very small; L2 smaller and somewhat anterior to L1; SV1 relatively long (Fig. 8). On the second abdominal segment, D2 is slightly above D1; SD1, L1 and L2 equidistant from spiracle; SD1 and L2 in front of spiracle; L1 behind spiracle; L3 below and slightly posterior to L2; SV3 behind and level with L3; SV1 below and in front of SV4 (Fig. 7). Sixth abdominal segment with D1 above D2; SD1 directly below D1 and above anterior margin of spiracle; L2 directly below SD1 and just below spiracle; L1 behind spiracle and slightly more removed from spiracle than are SD1 and L2; L3 in front of L2 (Fig. 6). On eighth abdominal segment, D1 on prominent tubercle; SD1 and D2 level with each other; SD1, L2 and L1 arranged around spiracle as on sixth abdominal segment; SV3 slightly anterior to L1; SV1 directly below SV3 (Fig. 6). Abdominal segment 9 with D1, SD1 and L1 each somewhat anterior to the seta above; SV1 posterior to L1 (Fig. 6). Segment 10 with SD1 and D1 widely separated; D2 equidistant between L1 and adjacent D2; CP1 above CP2; Lg1, Lg2 and Lg3 in vertical line; CD1 above CD2 (Figs. 6, 11). On abdominal segments 1 and 2, 1
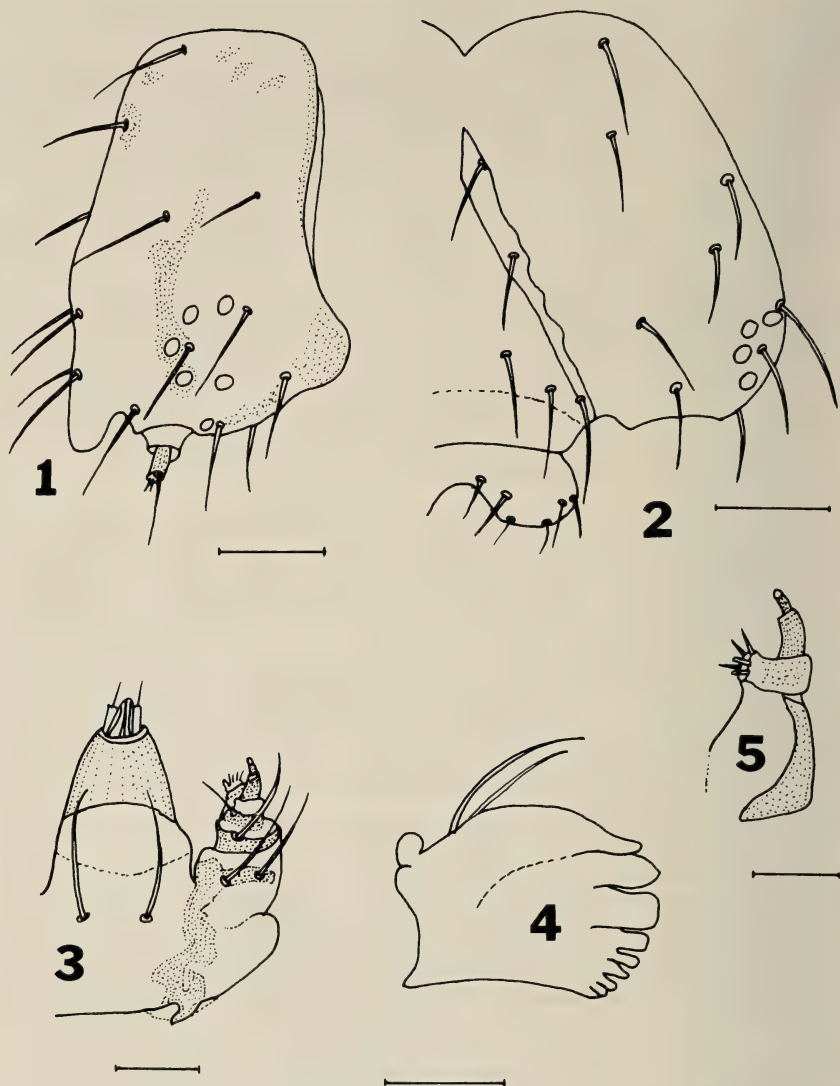
FIGS. 1–5. *Phigalia strigateria* larval head structures. Scale line length in parentheses. **1,** Lateral view of head (0.5 mm); **2,** Frontal view of head (0.5 mm); **3,** Ventral view of mentum, hypopharynx, labial palpi, spinneret and maxilla (0.25 mm); **4,** Inner view of right mandible (0.25 mm); **5,** Ventral view of maxilla (0.25 mm).

ventral seta is present; on segment 8, SV1 and SV4 closely adjacent (Fig. 12). The following chalazae are most prominent on last instar larvae: D2 and L1 on abdominal segments 2 and 3, and D1 on segment 8. Secondary setae numerous, especially dorsally and laterally on all segments; setae are fine, irregular and about ⅓ the length of primary setae. Body roughened with microspines anteroventrally on prothorax and ventrally on mesothorax.
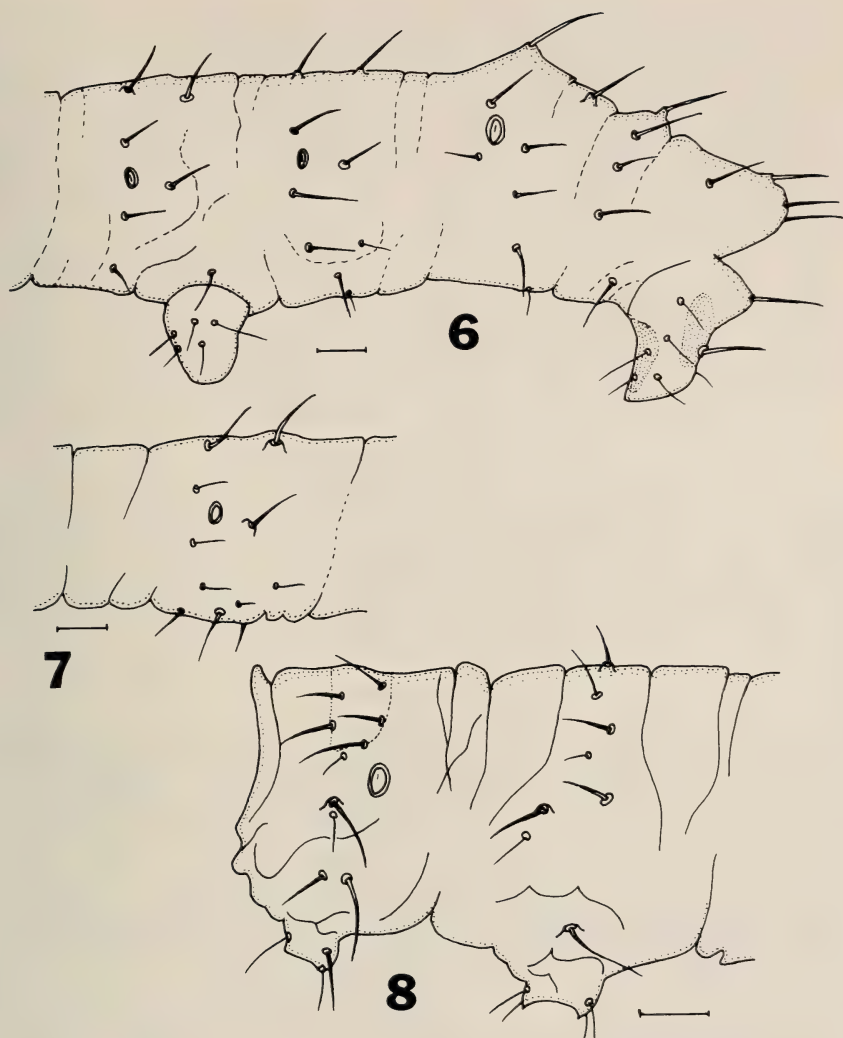
FIGS. 6–8. *Phigalia strigateria* larva. Scale line = 0.5 mm. **6,** Lateral view of abdominal segments 6–10; **7,** Lateral view of abdominal segment 2; **8,** Lateral views of pro- and mesothorax.

Mouthparts: Mandibles with 4 large and 5 small teeth, more basal mandibular seta longest (Fig. 4); postmentum with a pair of long setae (Fig. 3); hypopharynx heavily sclerotized; spinneret tubular in shape, slightly tapering apically; labial palps almost the length of spinneret (Fig. 3); ventral side of each maxilla with 4 prominent setae, most apical one smallest (Fig. 3); terminal lobe of maxilla with 3 setae and 2 elongated papillae, apicalmost seta longest (Fig. 5).

General: Last instar about 26 mm long and 3.1 mm wide; thoracic leg claw dark brown, pointed with 1 dorsal simple seta and 3 lateral and ventral bladelike setae (Fig. 13); A6 crochets a biordinal mesoseries in unbroken band.
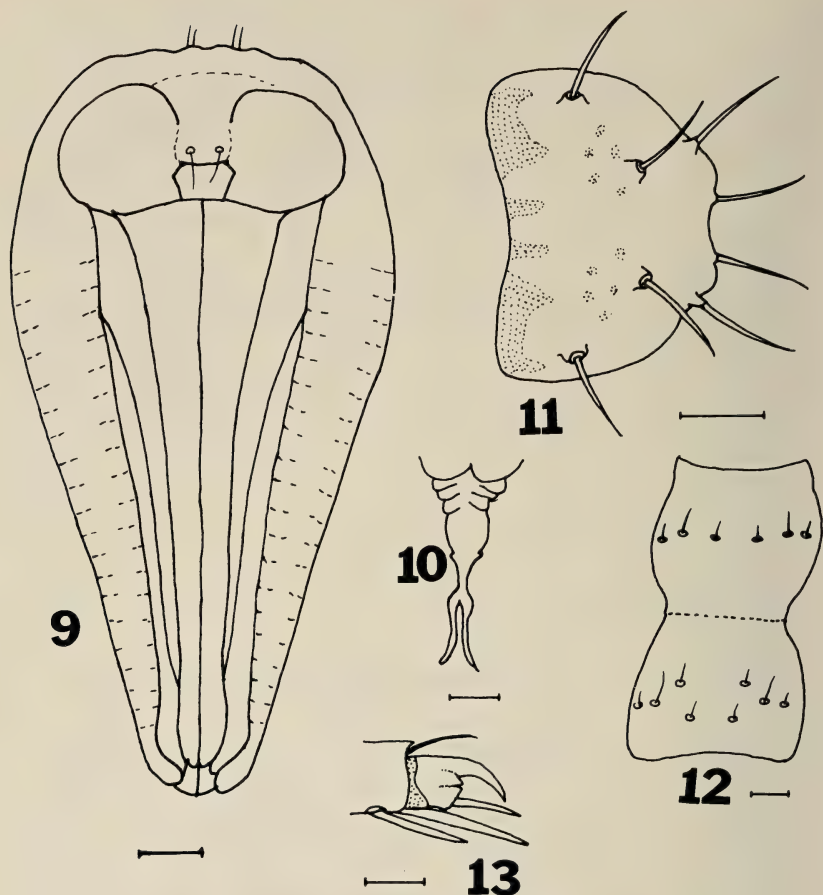
FIGS. 9–13. *Phigalia strigateria* larva and pupa. Scale line length in parenthesis. **9,** Pupa, ventral view (0.5 mm); **10,** Pupal cremaster (0.25 mm); **11,** Anal plate (0.5 mm); **12,** Ventral view of A1 and A2 (0.5 mm); **13,** thoracic leg claw (0.1 m).

Pupa. Reddish brown; eyes large, completely exposed, rounded; labrum hexagonal; maxillae slightly shorter than antennae; prothoracic leg extending about ⅕ length of maxilla, prothoracic femur not exposed; mesothoracic leg ending near antennae; metathoracic legs exposed beyond apex of maxillae (Fig. 9). Cremaster always bifurcate, spines usually asymmetrical (Fig. 10). Segment 7 constricted apically; abdominal segments coarsely punctate. Length similar for male and female, mean 9.9 mm (range 6.5–12) (43n); female stouter.

DISCUSSION

The chaetotaxy of mature *P. strigateria* larvae shows some variation in location of the following setae: P1 and A2 setae on head more medial than shown; L2 on abdominal segment 2 slightly before spiracle; anal plate with D2 setae closer to each other than to their respective L1's.

Comparison of *P. strigateria* larvae with those of *P. titea* from the same study areas in West Virginia showed close similarity in location of primary setae between the two species. Primary setae of *P. titea* are longer with most arising from small but well defined chalazae. SD1 and L2 on the prothorax are smaller in *P. titea* than in *P. strigateria*. Secondary setae of *P. titea* are shorter and sparser than those of *P. strigateria*. All body cuticle of *P. titea* is densely covered with microspines. Because of the marked color differences in larvae of the two species, they cannot be confused.

The pupa of *P. titea* is larger than that of *P. strigateria* (Butler 1985a). The labral shapes are more rounded than those of *P. titea*. *Phigalia titea* vertex lacks the prominent rugosity of *P. strigateria*; frontoclypeal area is smooth in *P. strigateria*, rugose in *P. titea*.

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TRAP PREFERENCES OF *RETINIA METALLICA* AND SEASONAL FLIGHT BEHAVIOR OF *RETINIA* SPP., *RHYACIONIA* SPP. (TORTRICIDAE), AND *CHIONODES* SPP. (GELECHIIDAE) IN THE DAKOTAS

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ABSTRACT. At high population levels, white and green traps baited with (Z)-7-dodecenyl acetate caught more *Retinia metallica* than blue traps. Diamond-shaped traps were more effective than cup traps, but did not differ significantly in effectiveness from triangular-shaped traps. *Rhyacionia fumosana* and *R. neomexicana* responded throughout May to synthetically-baited traps. *Rhyacionia bushnelli* and *Retinia metallica* flew in late May or early June.

Tip mining lepidopterous larvae can cause extensive damage to ponderosa pine (*Pinus ponderosa* Laws.) in the northern Great Plains (Stein & Kennedy 1972). Information on their distribution is limited; effective techniques for detecting and evaluating infestations are not available (Dix et al. 1984). Accurate determination of the flight period of Lepidoptera that are concealed for most of their life cycle is crucial to the effective timing of insecticide applications. Sex attractants are ideal for detecting and delineating the adult flight period of such Lepidoptera (Stevens et al. 1980). Jacobson and Jennings (1978) and Stevens et al. (1980) identified attractants of *Rhyacionia fumosana* Powell and *Rhyacionia neomexicana* (Dyer). Several possible lures of *Retinia metallica* (Busck) and *Rhyacionia bushnelli* (Busck), two of the more common species in the north central U.S., were identified by Dix et al. (1984). A trapping technique for *Retinia metallica* using these lures needs to be refined. This article describes trap design and trap color preferences of *R. metallica,* and delineates the flight period of *Retinia* spp., *Rhyacionia* spp. (Tortricidae: Olethreutinae), and *Chionodes* spp. (Gelechiidae) that infest ponderosa pine in North Dakota and South Dakota.

TABLE 1.   Description of sites used to determine flight periods of pine-feeding Lepidoptera in North Dakota and South Dakota, 1973–76.

Year	Locality	Type of stand	Tree height (m)	Estimated number of trees	Trapping period
1975	Near Burning Coal Vein, Little Missouri Grasslands, Custer National Forest, Slope Co., North Dakota	Native	0.5–20	500	10 May–20 July
	North Cave Hills, Custer National Forest, Harding Co., South Dakota	Native	0.5–20	500	10 May–20 July
	Slim Buttes, Custer National Forest, Harding Co., South Dakota	Native	0.5–20	500	10 May–20 July
	Big Sioux Conifer Nursery, Coddington, Co., South Dakota	Planted	2–6	3,000	8 May–15 June
1976	Near Burning Coal Vein, Little Missouri Grasslands, Custer National Forest, Slope Co., South Dakota	Native	0.5–20	500	10 May–3 Aug
	Big Sioux Conifer Nursery, Coddington Co., South Dakota	Planted	2–6	3,000	27 May–22 June

METHODS AND MATERIALS

Trap design and trap color preferences of *R. metallica*. Trials were conducted in May and June at the Big Sioux Conifer Nursery, Coddington Co., South Dakota. Initially, a moderate population (5 pitch blisters/tree) was present in the 9-year-old ponderosa pine provenance planting, and a high population (36 pitch blisters/tree) was present in the 20-year-old ponderosa pine in the nursery's border planting.

A cardboard cup trap (0.24 liter), a triangular milk carton trap (9 cm high and 15 cm long), and a diamond-shaped milk carton trap (9 × 9 × 15 cm) were each lined with Stikem Special® and were baited with 10 mg of (Z)-7-dodecenyl acetate. All traps were open at both ends and were white. There were six blocks of three traps (one of each design). Traps in each block were hung in the border planting 20 m apart at a height of 1.5 m.

The effect of trap color on trap catch was determined with diamond-shaped traps painted white (2A1), pale blue (24A5), green (28D8), or fluorescent orange (7A8). Notations following colors refer to Kornerup and Wanscher's (1967) standard colors. All traps were baited with rubber septum dispensers containing 10 mg (Z)-7-dodecenyl acetate plus 10 mg trioctanoin and were deployed 20 m apart at a height of 1.5 m in perimeter ponderosa pines. There were six blocks of four traps (one of each color) in trial 1 and four blocks of four traps in trial 2.

TABLE 2. Comparison of trap catch of male *R. metallica* with different sticky trap designs baited with 10 mg of (Z)-7-dodecenyl acetate plus 10 mg trioctanoin.

Design	Surface area (cm²)	Number of traps	No. males/trap		No. males/cm²	
			Mean[1]	SE	Mean[1]	SE
Diamond	427.5	3	187a	21.4	0.5a	0.05
Triangular	405.0	3	142ab	28.4	0.3a	0.06
Cup	220.5	3	59b	4.3	0.3a	0.02

[1] Means followed by the same letter are not significantly different (P < 0.05) according to Tukey's procedure for multiple comparisons.

Each week for three weeks, trap catches were counted and the traps were randomly reassigned to a new site within the block. Analysis of variance and Bartlett's test for homogeneous variance were performed on the total catch per trap. When necessary, the data were transformed by $\ln(x + 1)$ to stabilize the variance for analysis of variance. Tukey's honestly significant difference procedure at the 5% level was used to separate means (Sokal & Rohlf 1969).

Seasonal flight record. During spring and early summer of 1975 and 1976, known attractants of *Rhyacionia* spp. and *Chionodes* spp., and several related synthetic compounds were used to attract *Rhyacionia* spp., *Retinia* spp., and *Chionodes* spp. that damaged ponderosa pine in native and planted stands (Table 1). Compounds used as lures included (E)-7-decenyl acetate, (Z)-7-decenyl acetate, (E)-7-dodecenyl acetate, (Z)-7-dodecenyl acetate, (Z)-7-dodecen-1-ol, (E)-8-dodecenyl acetate, (Z)-8-dodecenyl acetate, (Z)-9-dodecenyl acetate, (E)-9-dodecenyl acetate, (E)-9-dodecen-1-ol, (Z)-10-dodecenyl acetate and (E)-10-dodencenyl acetate. In 1975, each compound was replicated twice at a site, and traps and dispensers were changed three times during a trapping period. In 1976, each compound was replicated five times at a site, and traps were changed six times at two-week intervals during a trapping period.

Traps were cardboard cups (0.24 liter) with a 2.5 cm diameter opening at both ends. The inside was coated with Stikem Special®. In 1975, a cotton wick dispenser (12 × 10 mm) was impregnated with 20 mg of a test compound and placed in the bottom of each trap. In 1976, a rubber septum dispenser (5 × 9 mm) baited with 10 mg of test compound was used. In 1975 and 1976, compound activity was prolonged by adding 10 mg of the extender trioctanoin. Control dispensers also were baited with 10 mg of trioctanoin and were replicated twice per site in 1975 and five times per site in 1976. Traps baited with synthetic attractants or with control dispensers were hung on ponderosa pine branches at a height of 1.5 m and a spacing of at least 20 m.

TABLE 3.   Effect of trap color on catches of male *Retinia metallica* in diamond-shaped sticky traps baited with 10 mg of (Z)-7-dodecenyl acetate plus 10 mg trioctanoin.

Trap color	Trial 1			Trial 2		
	Number of traps	No. males/trap		Number of traps	No. males/trap	
		Mean[1]	SE		Mean[1]	SE
White	4	150.3a	35.91	4	3.5a	1.19
Green	4	123.5a	34.50	4	2.5a	0.95
Orange	4	95.3a	44.18	4	1.8a	0.63
Blue	4	16.0b	2.16	4	0.8a	0.48

[1] Means followed by the same letter are not significantly different (P < 0.05) according to Tukey's procedure for multiple comparisons.

Captured moths were identified and counted when traps were changed. Moths were removed from traps with forceps or by carefully cutting the trap around the moth. Specimens were tentatively identified and numbers of moths per species were recorded. Representative samples of each presumed species were sent to specialists for identification.

RESULTS AND DISCUSSION

Trap design and trap color preferences of *R. metallica*. Traps in several blocks were blown down during a spring storm; catches in traps from these blocks were not included in analyses. The second color preference trial was conducted the following spring, after the number of active *R. metallica* had abruptly decreased (less than 1 pitch blister/tree). An unusually wet August and winter probably contributed to the high larval mortality and reduction in number of adults.

Effectiveness of the traps varied with design and color (Tables 2, 3). Diamond-shaped traps had the largest surface area and caught more moths than either triangular or cup traps. However, only mean catches per trap of the diamond-shaped traps and cup traps differed significantly. At high population levels, as exhibited in trial 1, white, green, and orange traps caught significantly more males than blue traps (Table 3). However, at low population levels (trial 2), trap color did not affect trap catch.

Seasonal flight behavior. The beginning and end of male flight for five species of Olethreutinae which infest the branch tips of ponderosa pine varied yearly with the onset of spring. For example, the spring of 1976 was warmer than in 1975, and moth flights of *Retinia metallica*, *R. gemistrigulana* and *Rhyacionia fumosana* were earlier (Fig. 1).

In southwestern North Dakota and northwestern South Dakota, male *R. fumosana* and *R. neomexicana*, the first species trapped in the
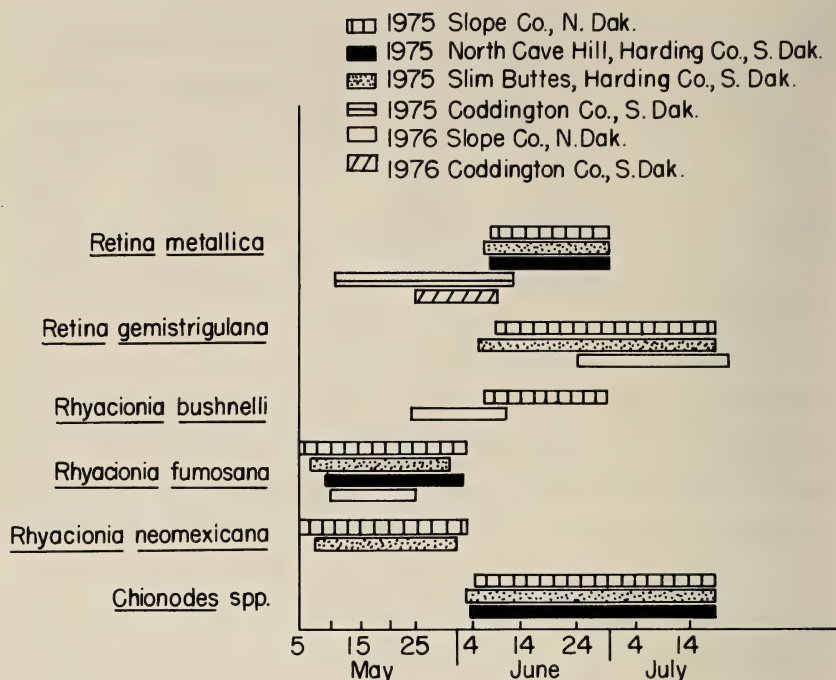
FIG. 1. Seasonal flight of Tortricidae: Olethreutinae and Gelechiidae that damage ponderosa pine in North Dakota and South Dakota.

spring, were usually caught in early May. *Rhyacionia bushnelli, Retinia metallica*, and *R. gemistrigulana* (Kearfott) were caught two to three weeks later, frequently in late May or early June. Large numbers of *Chionodes* spp. (Gelechiidae), which mine cones of ponderosa pine, were caught during June and July. Flight of *Retinia metallica* in northeastern South Dakota (Coddington Co.) was about two weeks earlier than in northwestern South Dakota.

In conclusion, white, green, or orange diamond- and triangular-shaped traps are effective in catching male *R. metallica*. However, diamond-shaped traps are preferred for future attractant trials and for detecting males because they provide a larger surface area. Time of moth flight varies annually. Additional research is needed to determine the effect of cumulative atmospheric and ground temperature on moth flight and to develop a method for accurately predicting moth flight.

tricidae; and R. W. Hodges, USDA, Agricultural Research Service, Northeastern Regional Agricultural Research Center, Beltsville, Maryland, identified the Gelechiidae.

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LIFE HISTORY OF *NEMORIA GLAUCOMARGINARIA* (BARNES & McDUNNOUGH) AND LARVAL TAXONOMY OF THE TRIBE NEMORIINI (GEOMETRIDAE: GEOMETRINAE)

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ABSTRACT.   Morphology, chaetotaxy, and color pattern of immature *Nemoria glaucomarginaria* (Barnes & McDunnough) are described for the first time. Large dorsolateral projections on the middle abdominal segments provide crypsis on the host plant (*Quercus* spp.), enhanced by a "shaking" behavior while moving. Larval color pattern of *N. darwiniata punctularia* Barnes & McDunnough is also figured, and two new hosts are reported (*Arctostaphylos* sp. and *Ceanothus cordulatus* Kell.). The description of *glaucomarginaria* is used as the basis for recognition of the genus *Nemoria*. A preliminary key to larvae of the four genera in the tribe Nemoriini is presented, based on fourteen species.

Taxonomy of the Geometrinae based on adult genital morphology has been covered in detail by Ferguson (1969, 1985). His studies reveal a remarkable array of parallelisms and convergences in the facies of adults. Individuals from different species groups within genera, or even from different tribes, have routinely been classified as conspecific in major museum collections. For example, *Nemoria glaucomarginaria* (Barnes & McDunnough) of the *bistriaria* group is often found with *N. darwiniata* (Dyar) of the *obliqua* group, and species of *Dichordophora* Prout (Dichordophorini) are often found with *Dichorda* Warren (Nemoriini). Although the taxonomic groupings outlined by Ferguson are well defined, their interrelations remain unknown. Adult characters present numerous problems for phylogenetic reconstruction: the "superficial" characters show many parallelisms, convergences, and plesiomorphies, while the genitalia are so different between tribes and so similar within genera that most phylogenetic information is lost. However, the larvae show remarkable adaptations for crypsis, and may give information of phylogenetic significance not present in the adults.

This paper describes the larva and life history of *Nemoria glaucomarginaria* and uses this information as the basis for the generic recognition of *Nemoria* larvae. It concludes with a preliminary key to the genera of nemoriine larvae.

MATERIALS AND METHODS

Gravid females of *N. glaucomarginaria* and *N. darwiniata punctularia* Barnes & McDunnough were collected at ultraviolet and visible wavelength fluorescent lights from the following California localities in 1984 and 1985: *glaucomarginaria*: Gold Run, Placer Co.; Washing-

ton, Nevada Co.; Rubicon River Cyn., 1.5 km N Uncle Tom's Cabin, El Dorado Co.; Barton Flats, San Bernardino Nat. For., San Bernardino Co.; *d. punctularia*: Santa Rosa, Sonoma Co.; Baxter, Placer Co.; Meeks Bay, El Dorado Co.; Carson River Cyn., Alpine Co.; Mill Ck. (Lundy Cyn.), Mono Co. Additional preserved material of *d. punctularia* was examined from Ash Cyn., Huachuca Mts., Cochise Co., Arizona.

Ova were collected from moths confined in inflated, resealable plastic sandwich bags. Larvae were reared on foodplant cuttings in similar containers at 25°C under natural photoperiods throughout spring and summer. Specimens of each stage and instar were preserved in KAAD before transfer to 95% ethyl alcohol. Color photographs were taken of the ultimate instars. Figures were drawn with the aid of a camera lucida, with color patterns added freehand from the color slides. Chaetotaxy follows McGuffin (1964, 1967, 1977).

More than 100 larvae were reared to adults. Five specimens of each stage were examined for morphological details. Colors are described from two specimens of each species exhibiting the most common coloration. Colors should not be relied on for specific identification.

Larvae of additional species used in constructing the key are from personal rearings or from the collection of Noel McFarland. The species examined were *Nemoria pulcherrima* (Barnes & McDunnough), *N. unitaria* (Packard), *N. arizonaria* (Grote), *N. festaria* (Hulst), *Chlorosea margaretaria* Sperry, *C. roseitacta* Prout, *C. banksaria gracearia* Sperry, *Dichorda consequaria* (Hy. Edwards), *D. illustraria* (Hulst), and *Dichordophora phoenix* (Prout). An additional undetermined larva from near Valyermo, Los Angeles Co., California, was also examined; it is probably *N. intensaria* (Pearsall). Specimens used in formulating these descriptions will be deposited in the Bohart Museum (University of California, Davis) and in the McFarland Collection.

Nemoria glaucomarginaria (Barnes & McDunnough)

Egg. Ovate, 0.7 mm long by 0.5 mm wide, with flattened, slightly concave top; vertical sides 0.2–0.3 mm thick, with sharp edge between sides and top; decorated with small ridges in an irregular reticulate hexagonal pattern. Yellow when laid, gradually darkening through orange to dark red over a period of 9–12 days, becoming translucent 2 days before hatch. Larva emerges through hole chewed in side wall at anterior end. A photograph of the related *N. darwiniata punctularia* (Comstock & Henne [1940], as *pistacearia* [Packard]) is representative of *glaucomarginaria*, as well as all *Nemoria* examined to date. Details of microstructure of *glaucomarginaria* eggs were not examined, but seem to agree with those of *N. bistriaria rubromarginaria* (Packard) (Salkeld 1983:153). Clutches of up to 55 eggs were recorded.

First instar. Similar to ultimate instar (Fig. 1), but with dorsolateral projections on A2–4 smaller, thicker, and squared off; setae L1 and L2 at tips. Projections half as wide as segments anteroposteriorly (*Dichorda* are ¾ as wide in the first instar). Color mottled brown, pattern obscure; setae clear and blunt. Head width 0.3 mm, body length 3 mm at hatch. Chaetotaxy not examined.

Second instar. Like first instar, except dorsolateral projections on A2–4 slightly more
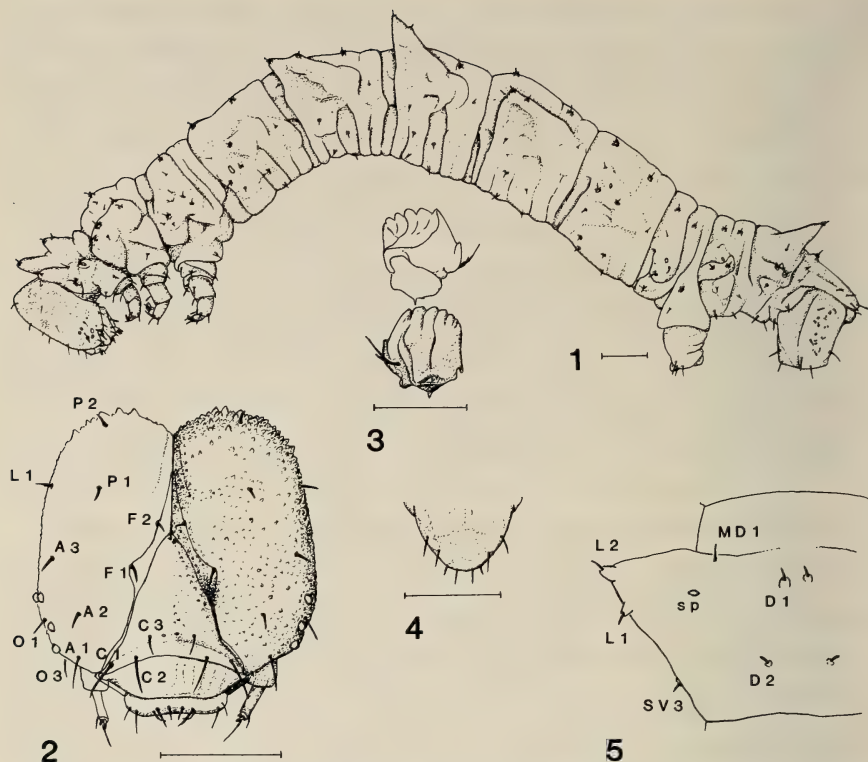
FIGS. 1–5. *Nemoria glaucomarginaria*, scale 1 mm, except as indicated. **1,** Morphology of fifth instar, lateral view; **2,** Head of fifth instar. Pattern of larger spicules and darker markings at right, chaetotaxy at left. Setae translucent; **3,** Right mandible. Internal aspect unshaded, external shaded. Scale 0.5 mm; **4,** Anal shield, dorsal view; **5,** A3, dorsal view, showing placement of setae and spiracle.

elongate at L2 than L1. Color mottled brown, gross elements of fifth instar pattern sometimes visible posteriorly and dorsally.

Third instar. Structurally identical to fifth instar; coloration as in second instar, except pattern elements usually more visible.

Fourth instar. Identical to fifth instar, except in size.

Fifth instar. The following description is given by segment.

Head (Fig. 2) width 2.1–2.5 mm; tan to brown, mottled with darker pigment as shown; covered with spiculiferous projections containing white pigment spots under a clear cuticle, spicules reaching greatest devlopment on dorsal epicranium. Setae translucent, not black as shown. Clypeus lighter than head, with wrinkles as in *d. darwiniata* (Dyar 1904). Mandibles as illustrated (Fig. 3).

The following descriptions refer to Figs. 1, 8, and 10, except as indicated:

T1 with dorsal conical projections bearing setae XD1 and XD2; caudad another projection bearing setae D1 and D2 together. Another swelling dorsolaterally bears setae L1 and L2; SV2 and SV3 on swelling above leg. L2 long and hairlike, probably acting as a proprioceptor. Pattern as figured, colors light to very dark brown, with whitish markings; addorsal line often dark green. **T2** with large protuberance elevating setae L1–3, SD1, and SV3; SV2 on swelling above leg. SD2 long and thin. Color as in T1. **T3** structure as
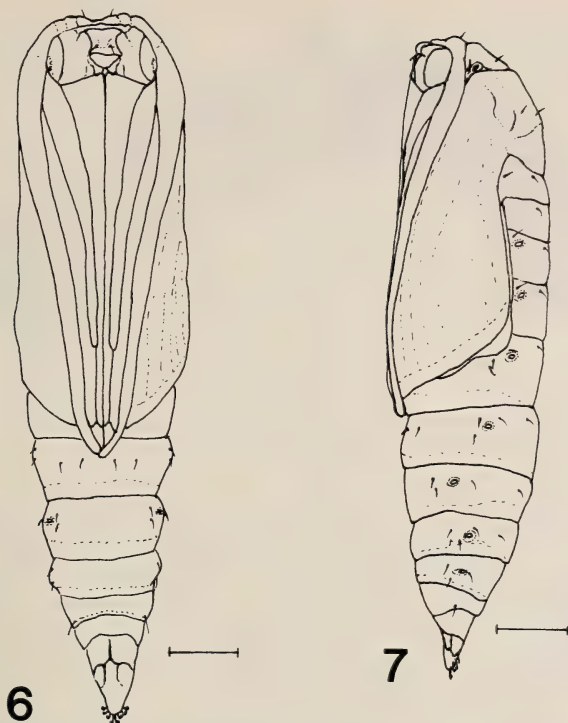
FIGS. 6, 7. *Nemoria glaucomarginaria* pupa. **6,** Ventral aspect; **7,** Lateral aspect.

in T2; green, resembling color of foodplant, especially posteriorly, with lighter markings as shown; protuberance light brown, dorsal markings green or brown.

A1 with D1 barely raised, closer to mid-dorsal line than D2. Lateral protuberance small, bearing SD2 only. Spiracle below protuberance, above L2 and L1. Color green with markings as shown; darker green shading below protuberance. Anterior mid-dorsal patch dark. **A2–4** (Fig. 5) with D1 as in A1, except raised more. Spiracle above projection; MD1 thin, anterior to spiracle, probably a proprioceptor. SD setae absent. Dorsolateral projections large, conical, slightly bidentate, bearing L2 at greatest extremity, L1 caudad; projections longer and more pointed on A3. SV4 on line between L3 and SV2 in segments A3 and A4. Pattern as shown; color brown on anterior part of segments and on distal half of projections, green elsewhere. A2 often completely brown as shown, A3 usually mostly green. White markings around anterior mid-dorsal patch, on caudal edge of projections, anterior subdorsal patch, and lateral line, pronounced in intersegmental areas; smaller whitish markings as figured. Adventral line dark, chainlike, often obscure. **A5** with D1 placed further from mid-dorsal line than on A1–4, still closer to mid-line than D2. SD setae absent. Lateral protuberance small, raising L1 and L2. Spiracle above protuberance. Color green, pattern as on A2–4, except anterior mid-dorsal patch obscure. **A6** with D1 and D2 equidistant from mid-dorsal line. SD setae absent. Small swelling below spiracle bearing L1 and L2. Crochets reduced to half length in center, not wholly interrupted. Pattern as shown; anterior green, posterior brown to purplish brown with frosty countershading on leg. **A7** with D1 and D2 equidistant from mid-dorsal line. SD setae absent. Small swelling below spiracle elevating L1 and L2. Pattern as shown; color light brown on swelling to dark brown generally, markings white; brown countershades
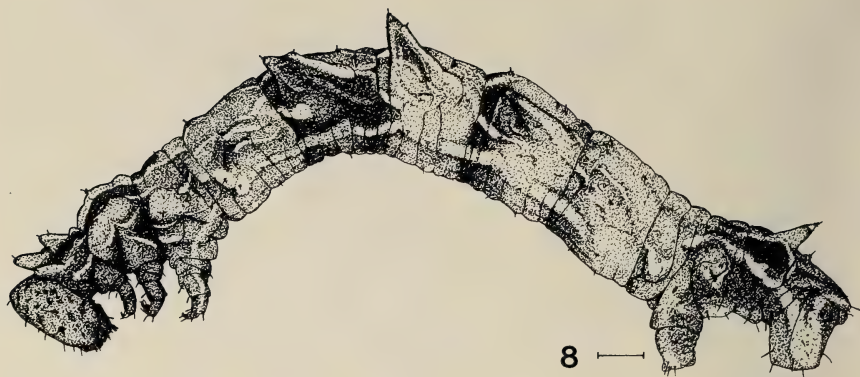
FIG. 8. *Nemoria glaucomarginaria*. Lateral aspect showing pattern of markings on fifth instar. Refer to text for color description. Scale 1 mm.

to whitish ventrally. **A8** with D1 raised dorsally on high conical projection directed caudally. Pattern as shown; projection light brown with whitish tip, dark chestnut brown on patch below this. Purplish brown below white subdorsal line, fading to whitish ventrally. **A9** with D1 on large chalaza; other setae as shown. **A10** with anal plate as shown (Fig. 4). Sclerotized shield of proleg marked with darkly pigmented indentations of various sizes (Figs. 1, 10), slightly variable in placement. An additional seta, herein named LG4, present on the anteroventral corner of shield (also present in all other *Nemoria* examined). Pattern as shown; markings white to buff on brown background. Crochets wholly interrupted in center by fleshy pad.

Entire surface of larva covered with spicules, each usually with white spot of pigment inside. They reach greatest size dorsally and on projections and protuberances, approaching length of blunt setae. Spicules smaller below, giving rugose, granular or velvety appearance; most without white pigment on segments A6–10. Most setae (except MD1) raised on chalazae (Fig. 10), which often accumulate spicules, especially dorsally.

A loose cocoon is spun on the foodplant along a twig, incorporating pieces cut from nearby leaves, or from cage material (such as cloth or paper).
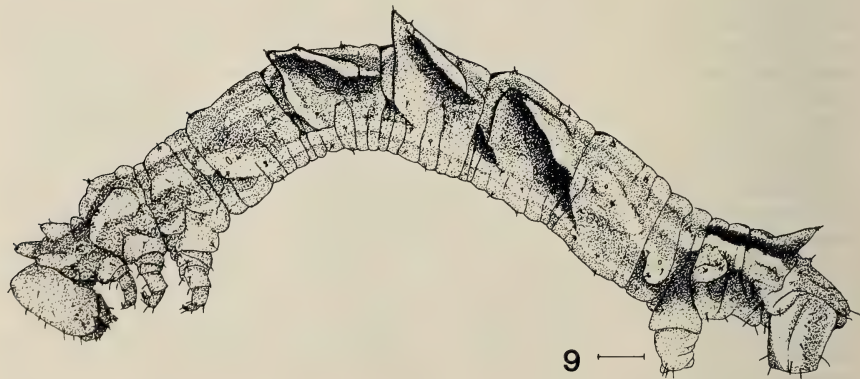
FIG. 9. *Nemoria darwiniata punctularia*. Lateral aspect showing pattern of markings on fifth instar. Refer to text for color description. Scale 1 mm.
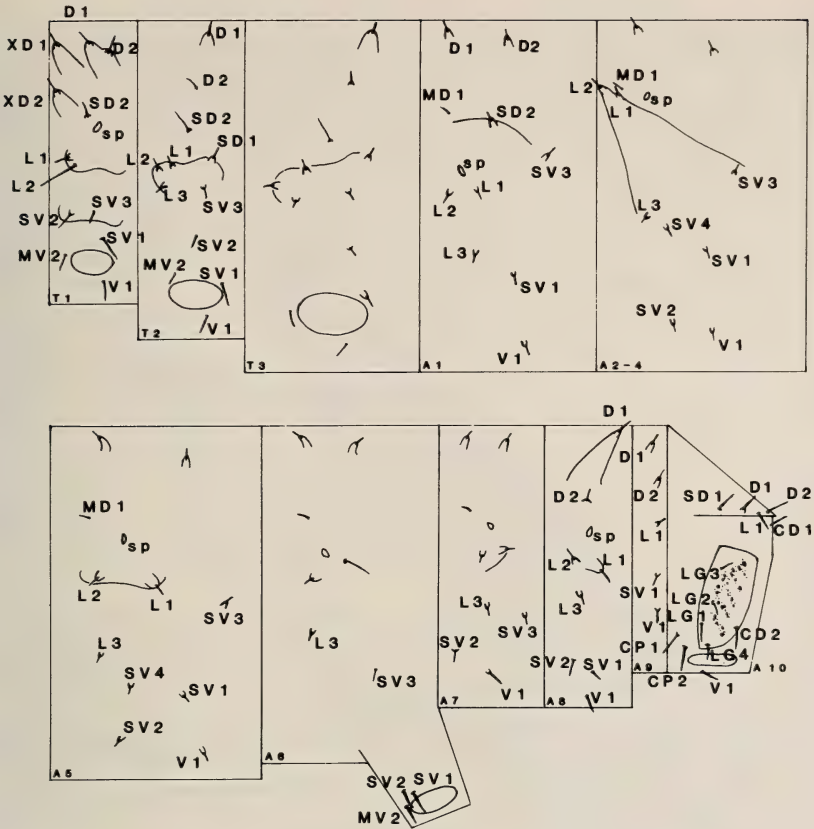
FIG. 10. Setal map of *Nemoria glaucomarginaria*.

Prepupa essentially a stout, compacted fifth instar larva. Dorsolateral projections gradually absorbed during 3- to 4-day prepupal period.

Pupa (Figs. 6, 7) unadorned except for light sculpturing about face and antennal bases. Wing cases extend to middle of A5; antennae and T3 legs often extend just beyond. Figs. 6 and 7 show range of observed variation in relative lengths of wing and antennal cases. Faint venation visible on wing cases. Single setae at bases of antennae, between antennae and eyes, on T1 anterior to spiracle and dorsally; 2 setae on T2; seta on each abdominal segment in a single dorsal row and spiracular group of 3; a pair on A6 ventrally. Cremaster usually with 8 hooks, longest distally; 7 or 6 in some individuals. Yellow at molt, coloring to tan; black markings dorsal to spiracles, surrounding prespiracular setae, and dotted on wing veins. Mid-dorsal line dark. Eyes darken after 6–8 days, wings color to green with lines visible in 10–15 days; abdominal spots visible 12–24 h before eclosion. Emergence at dawn or dusk; pupal duration 12–18 days, with males emerging first (protandry). Winter diapause probably occurs as pupa, but this has not been verified, and at least some Nemoriini and Synchlorini diapause in third instar.

Pattern markings on larvae remarkably constant, although degree of pattern expression varied slightly, and coloration varied considerably. Larvae reared during summer on *Quercus suber* L. (Fagaceae), a Mediterranean species with grayish foliage, showed little pattern, resulting in mostly gray-green larvae. Those reared in spring on *Q. lobata* Nee.,

a native species, showed greatest contrast, resulting in green and brown mottled larvae. Whether this effect is genetic, seasonal, or a reaction to foodplant is unknown.

Host plants. No wild collected larvae are known. All larvae were reared on new shoots of *Quercus* spp. available in Davis, California. *Quercus agrifolia* Nee., *Q. lobata,* and *Q. suber* were readily accepted. I often collected adults in association with *Q. kelloggi* Newb. in numerous localities in the Sierra Nevada and San Bernardino Mts. Material from Los Molinos, Tehama Co., in the northern Central Valley, probably fed on *Q. lobata,* the only oak species native to that area (Griffin & Critchfield 1976). Those collected at Norden, Nevada Co., California probably use *Q. vaccinifolia* Kell., the only oak in that area (A. M. Shapiro, pers. comm.). Those from coastal Orange and San Diego counties must have fed on *Q. agrifolia,* or on an ornamental species, for the same reason (Griffin & Critchfield 1976, Munz & Keck 1968). Five larvae fed *Salix hindsiana* Benth. (Salicaceae; a species acceptable to *darwiniata*) died in third instar.

Behavior. All instars exhibited the often described "shaking" behavior, imitating a piece of dried plant material in a light breeze. This behavior is common to all Nemoriini and Synchlorini reared to date, but is apparently absent in the Hemitheini. First and second instars were observed with bits of food and fecal material attached to the body, a common behavior of the Synchlorini. Closer examination revealed that this adhered due to high humidity in the rearing containers, and not by silken threads as in the Synchlorini. The larvae did not replace removed material, and larvae reared in drier containers showed no attached materials. Young larvae, and to some extent even mature larvae, showed a marked tendency to remain feeding in the same place even if the food began to deteriorate. This behavior appears to be adaptive; dead plant material is typically associated with caterpillar herbivory, and larvae may enhance crypsis by remaining at the feeding site.

Distribution. Records are scattered throughout California west of the Great Basin (Fig. 11). The species is also distributed northward through the Coast Ranges and Cascades to British Columbia (Ferguson 1985). The dense cluster of points in S California, the San Francisco Bay area, and in the Sierra Nevada from El Dorado to Plumas counties are no doubt attributable to differences in collecting intensity. I am responsible for much of the cluster W of Lake Tahoe. The only dubious record shown is of two specimens in the Bohart Museum from Alturas, Modoc Co., California, in the NE corner of the state. These were part of a large light trap sample at the Agricultural Inspection Station (J. S. Buckett, pers. comm.). There are no native oak species within 60 km of that locality (Griffin & Critchfield 1976), implying that the specimens were probably either carried in on a vehicle or mislabelled.

Phenology. *Glaucomarginaria* has 2 generations annually in northern California at low to mid elevations, one flying in mid-May and one in early July. These dates are variable depending on elevation and season. Ferguson (1985) reports slightly earlier dates in southern California. Adults of the spring brood may be collected when the leaves of the foodplant begin to unfurl. I have only encountered one generation at Norden, Nevada Co., elevation 2,140 m.

Nemoria darwiniata punctularia Barnes & McDunnough

Color pattern of the mature larva of *N. darwiniata punctularia* Barnes & McDunnough is shown in Fig. 9. This species has been figured (Comstock & Henne 1940, as *pistacearia*), but the reproduction lacks details for specific identification. *Nemoria darwiniata punctularia* is usually paler than *glaucomarginaria,* typically yellowish green, with medium brown markings and whitish lines. The body is slightly stouter, and projections correspondingly shorter. The spicules tend to be smaller and more even in size, giving a more velvety appearance than *glaucomarginaria.* The differences, however, are so slight that I use a tracing of Fig. 1 (*glaucomarginaria*) to illustrate the *d. punctularia* pattern. Fig. 9 also agrees with Dyar's (1904) written description of *d. darwiniata* (Dyar) from British Columbia. The third instar has the same pattern of markings, but is brown from the lateral line dorsally to beneath the protuberances, giving the aspect of a serrate brown line on the side of the body.
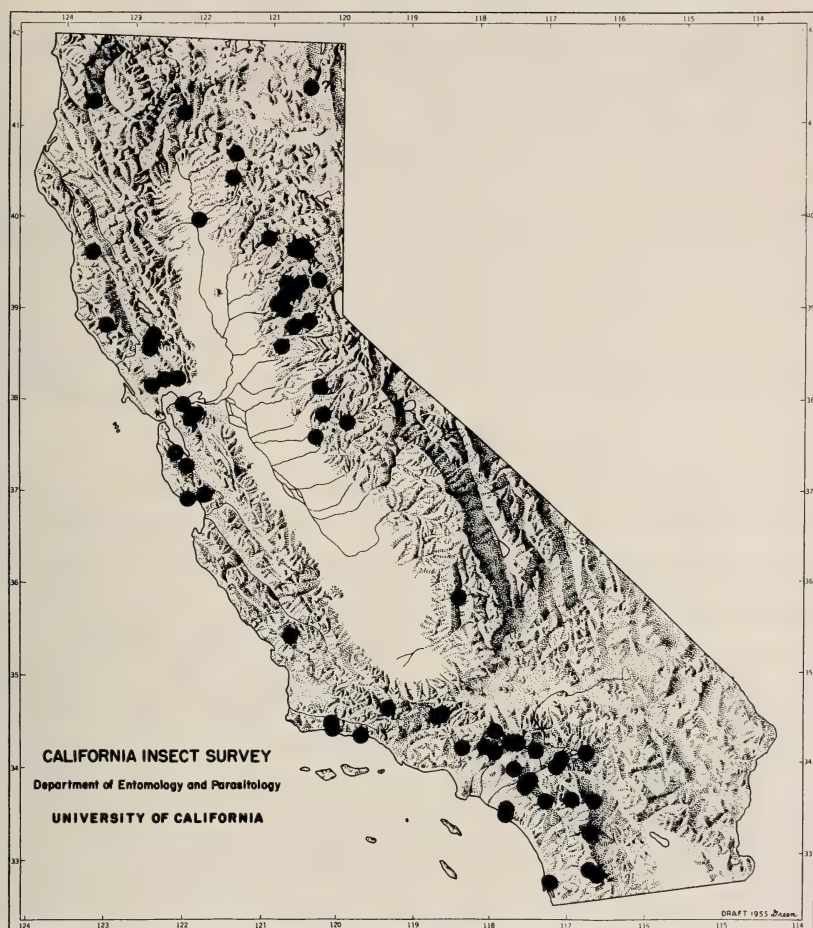
FIG. 11.   Distribution of *Nemoria glaucomarginaria* records in California.

These two species are most distinguishable by pattern. In general, the anterior of each abdominal segment is most contrasting in *glaucomarginaria*, while the posterior of each segment is most contrasting in *darwiniata*. *Glaucomarginaria* larvae appear to be indistinguishable in color pattern and morphology from *Nemoria festaria* from the mountains of S Arizona to Texas. Female genitalia are also very similar between these two species (Ferguson 1985). *Darwiniata* is apparently at least oligophagous, being reared from *Salix* (Salicaceae) (Dyar 1904, pers. obs.), *Quercus* (Fagaceae) (Comstock & Henne 1940), and *Arctostaphylos* (Ericaceae) (N. McFarland notes in Los Angeles Co. Museum of Natural History) in the laboratory. I have also recorded it in

the field from *Ceanothus cordulatus* Kell. (Rhamnaceae) at Alpine Meadows, Placer Co., California (subsequently reared *ex ova* on this host in the laboratory).

Most larvae of the genus *Nemoria* examined agree in detail with the setal map of Fig. 10, although size and shape of projections and protuberances differ in minor details. Thus, the above morphological description of *N. glaucomarginaria* serves as a working description for the genus. The only exceptions known are discussed in the key below.

Discussion

Ferguson (1985) published the most accurate figure of a *Nemoria* larva to date. A clear figure of *Dichorda* was given by Comstock (1960). No figures of *Chlorosea* and *Phrudocentra* Warren (Nemoriini), or *Dichordophora* (Dichordophorini) have been published.

Nemoriine larval descriptions in most early publications focus on the bizarre morphological adaptations for crypsis and are of little value for taxonomic purposes at the species level. Moreover, because of the difficulties in identifying adults before Ferguson's (1969) revision, descriptions for most taxa need to be verified, and host records confirmed. As early workers did not have a broad range of species for comparative purposes, early figures such as those of Dammers are often misleading, as for example, his figure of *N. leptalea* (=*delicataria* Dyar) compared to the photograph in the same publication (Comstock 1960). His figure of *N. pulcherrima* (=*naidaria* Swett) is stylized as well (Comstock & Dammers 1937). Dethier (1942) figured the ultimate instar of *N. rubrifrontaria* (Packard) with long primary setae (of which some appear to be missing), a condition common to the Synchlorini, but unknown elsewhere in the Nemoriini. Rindge (1949) used Dethier's description as a basis of comparison for a preliminary generic description of *Chlorosea* which is correspondingly inaccurate.

The following key will serve to rectify some of these errors. It is of course preliminary in that it is not based on all the species, but it will serve to sort out some of the characters for a future phylogenetic analysis of the group.

Preliminary Key to Genera of Nemoriine Larvae

1. Dorsolateral projections on A2–6 wide, rectangular, and lamellate; setae on the outer corners (L1 & L2) and another (SD2) on the anterior edge of each plate .... *Dichorda*
1'. Dorsolateral projections on A2–6 conical, not wide and platelike as above 2
2. Dorsolateral projections on A2–4 tridentate, bearing three setae (SD2, L1, L2); the middle seta (L2) extending farthest from the body .... *Phrudocentra**

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* Based on the description of *Phrudocentra* in Ferguson (1985), as I have not seen larvae of this genus. *Dichordophora* (Dichordophorini) also keys out here. These two genera may be separated by locality if adults are not available:

2'. Dorsolateral projections bidentate, bearing two setae 3
3. Dorsolateral projections on A2–4 with posterior seta (L1) extending farthest from
    body; mid-dorsal projections well developed, bearing both D1 setae ... *Chlorosea***
3'. Dorsolateral projections on A2–4 with anterior seta (L2) extending farthest from
    body; mid-dorsal projections usually poorly developed of lacking .... *Nemoria****

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Dichordophora is a denizen of the desert areas of Mexico and SW United States, while *Phrudocentra* is from American subtropical and tropical regions.
** *Nemoria pulcherrima* also keys out here. The adult shows affinities to both *Chlorosea* and *Nemoria*, as well as some unique morphological and phenological characters (Ferguson 1985). I leave it here until more data pertaining to its taxonomic status can be gathered.
*** The single undetermined *Nemoria* larva mentioned earlier has a well developed mid-dorsal protuberance, in contrast to all other *Nemoria* examined (except *pulcherrima*). This may prove a phylogenetically useful character when more larvae have been described.

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GENERAL NOTE

MASS EMERGENCES OF THE PINE WHITE, *NEOPHASIA MENAPIA MENAPIA* (FELDER & FELDER), IN COLORADO (PIERIDAE)

Ferris and Brown (1981, Butterflies of the Rocky Mountain states, University of Oklahoma Press, Norman, 442 pp.) cite *Neophasia menapia menapia* (Felder & Felder) as an occasional economic pest in western montane forests, primarily of ponderosa pine (*Pinus ponderosa* Laws.) and lodgepole pine (*P. contorta* var. *latifolia* Engelmann). I observed mass emergences of this species in 1983 and 1984 in the pinon-juniper forest of western Colorado. The location was Eagle Co., White River National Forest, Frying Pan River Valley, 8.85 km E Basalt, ca. 2,196 m elev. In both years the emergence lasted 3 days; 13–15 August 1983 and 3–5 August 1984. The emergences were sudden, synchronized, truly massive in nature, and all the adults disappeared as abruptly as they appeared.

Earliest flight on calm, sunny mornings was recorded ca. 0745 h, and it was that of males typically searching for females around the high outer branch tips of mature pinon pine. Not until ca. 0900–0930 h did flight get fully underway, giving one the sense of the forest being alive with butterflies.

Feeding was never observed in spite of special efforts to confirm Ferris and Brown's observation of early morning nectaring at flowers, which were abundantly available throughout the area. The pinon-juniper association showed no evidence of damage by larvae, densities of which can only be imagined. Both tree species were growing vigorously, and the pinon were filled with developing green cones. Considering their apparent three-day life span and the lack of feeding, it seems possible that these adults are nonfeeders.

Male-to-female ratio of specimens collected was 5:1 (n = 58 in 1983, 72 in 1984), though I believe that to be distorted by my efforts to locate the rare females. A ratio of 50:1 is probably closer to the true situation. Females collected were so heavily gravid they struggled to fly.

In the 10 years I lived at this locality (1976–85) this population explosion of *N. m. menapia* occurred only during the aforementioned 2 years.

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SOD WEBWORMS: THE LARVA OF
MICROCRAMBUS ELEGANS (CLEM.)
(PYRALIDAE: CRAMBINAE)

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ABSTRACT.   Diagnostic characters of *Microcrambus elegans* (Clem.) larvae are given. The long flight period in S North America suggests there are several generations annually; in the north there appears to be only one. The larvae were reared artificially on corn silk.

Larvae of Crambinae are primarily grass feeders; some species severely damage lawns, meadows, and pastures. They have also been recorded damaging corn, oats, and wheat. Larvae of some species also feed on moss. Collections of adults are being made in E Ontario and W Quebec to obtain gravid females and to rear larvae from their eggs.

There are nine North American species of *Microcrambus*. None of the larvae have been described. *Microcrambus elegans* is the commonest and most widespread North American species of the genus. It occurs from Quebec S to Florida, and W to Kansas and Mississippi. In the northern part of its range, it flies from mid-June to late August, and probably only one generation occurs. In the south, it flies from March at least until October; there are probably several generations. *M. elegans* flies in late afternoon, early evening, and at night, coming commonly to light after dark. Adults appear in July and the first half of August in W Quebec and E Ontario.

Moths were captured by flushing them from grass. Females were confined in 28 ml (7 dram) 2.9 × 6.5 cm plastic vials with snap caps for oviposition. Strips (1.0 × 5.0 cm) of lightly moistened blotting paper were placed in vials to supply drinking water and humidity. Females readily oviposited in these containers. Adults remained alive for up to one week, and, in most cases, oviposited several times, depending on the freshness of the female, laying between 20–40 eggs each time. Eggs were laid singly, not covered by a sticky substance, and were easily transferred to 4.5 × 4.5 × 1.8 cm clear plastic boxes with tight fitting lids. The bottom of each box was covered with blotting paper which was lightly moistened daily using a spray bottle, and the eggs were examined at this time for visible changes. About 50 eggs were placed in each rearing container. The boxes were kept out of the sun. The eggs had an incubation period of seven to nine days at room temperature. The eggs are oval, creamy white when first laid, gradually turning yellow-orange at eclosion. Taxonomic and morphological
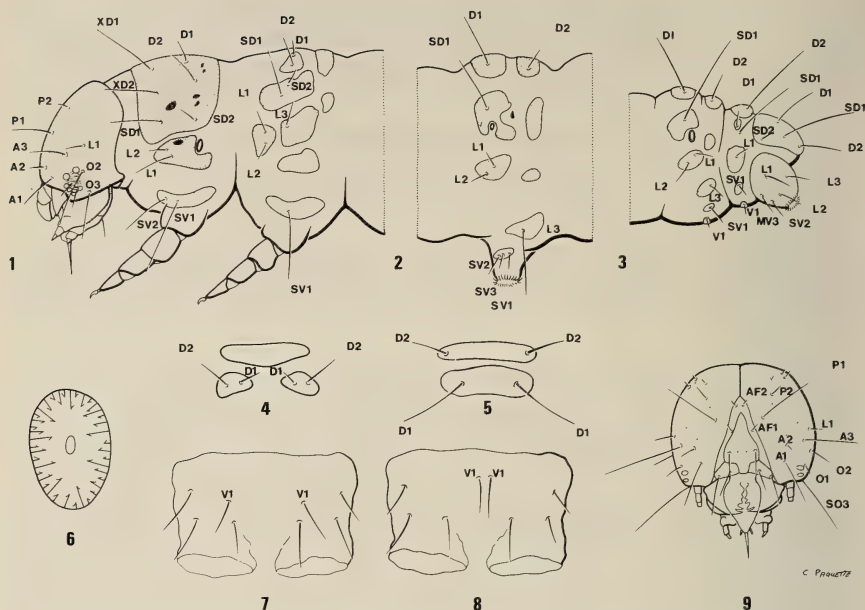
FIGS. 1–9. Larva of *Microcrambus elegans*, except where noted. **1,** Lateral view of head, prothorax and mesothorax; **2,** Lateral view of abdominal segment 4; **3,** Lateral view of abdominal segments 8, 9 and 10; **4,** Dorsal view of meso- and metathorax showing extra dorsal plate without setae; **5,** Dorsal view of abdominal segments 2–8 showing fusion of pinacula; **6,** Triordinal crochets; **7,** Ventral view of abdominal segment 10 of pyraustine larva showing setae V1; **8,** Ventral view of abdominal segment 10 of crambine larva showing setae V1; **9,** Anterodorsal view of head.

characters of the eggs as well as scanning electron micrographs of chorion sculpturing were given by Matheny and Heinrich (1972). When changes in the egg indicated that eclosion was about to occur, food was provided. Just enough food to cover the bottom of the rearing box was best; otherwise the first instars were difficult to locate.

Females from which eggs were obtained were deposited as voucher specimens in the Canadian National Collection (CNC). Some of the larvae were reared to adulthood so that male genitalia could be examined for positive identification. In general, however, the moth can be recognized by the brown horseshoe-shaped mark on the center of its folded wings. For detailed description and illustrations of the adult, see Felt (1894), Klots (1968), and Mauston (1970).

Larvae of *M. elegans* were successfully reared on corn silk, which, besides being nutritious, remains fresh longer than cut grass, and is tender enough for young larvae to bite. The clear hue of corn silk has an advantage over grass when it becomes necessary to find the first

instars, which are less than 0.5 mm long. The species of grass with which *M. elegans* is normally associated are not known.

DESCRIPTION

Hinton's (1949) system is used for the setae. Larvae of Crambinae can be recognized by the following characters: two prespiracular setae on prothorax (Fig. 1); a single transverse plate without setae posterior to dorsal pinacula on mesothorax and metathorax (Fig. 1); only one lateral seta on abdominal (A) segment 9 (Fig. 3); setae V1 on A10 half as far apart as on A9 (Fig. 8), as far apart or more than in most Pyralidae (Fig. 7); crochets triordinal, forming a complete circle (Fig. 6).

The larvae of *M. elegans* can be distinguished from other Crambinae by having pinacula D1 fused on dorsum of A1 to 8, and pinacula D2 fused on dorsum of A2 to 8 (Fig. 5), usually fused on dorsum of A1, but not always. The following description of last instar *M. elegans* includes only essential characters. Length 8–10 mm (N = 15). Head yellowish brown without markings. Stemmatal area black. Head setae as illustrated (Fig. 9). Body pale. Pinacula distinct, light brown. Prothoracic shield brown, with scattered dark spots. An extra dorsal plate without setae on mesothorax and metathorax (Figs. 1, 4). Two extra lateral plates without setae on mesothorax and metathorax (Fig. 1). Pinacula D1 fused on dorsum of A1 to 8 and pinacula D2 fused on dorsum of A2 to 8 (Fig. 5), usually fused on dorsum of A1, but not always. Pinaculum SD1 surrounding spiracle on A2 to 7 (Fig. 2). Two extra lateral plates without setae on A1 to 7 (Fig. 2), only one on A8 (Fig. 3). A black pit posterior to spiracle on proleg-bearing segments, probably indicative of tonofibrillary platelet (Fig. 2).

Material examined. Quebec: Lac-Ste-Marie, female collected 25 July 1984, 3 mature larvae, rearing SA-84-27, CNC Voucher 68. Ontario: 10 km W Richmond, female collected 1 Aug. 1984, 12 mature larvae, rearing SA-84-34, CNC Voucher 69.

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ULTRASTRUCTURE OF THE EGG OF THE AZALEA CATERPILLAR, *DATANA MAJOR* GROTE & ROBINSON (NOTODONTIDAE)

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ABSTRACT. Ultrastructure of the eggs of *Datana major* was studied by scanning electron microscopy. Eggs are spheroid (1.03 × 0.78 mm) but slightly broadened toward the base. The chorion surface is highly ornate with a rosette-mosaic pattern surrounding the micropyles. The lateral surface is covered with polygonal areas having aeropyles at the junctions of the ridges surrounding these areas. The presence of three micropyles arranged deltoidally appears to be unique among the Notodontidae.

Due to their importance as both a nursery crop and a landscape plant (Hill et al. 1985), greater attention has been placed on the insect associates of indica azaleas (*Rhododendron indica* (L.)). One serious defoliating pest of indica azaleas is the azalea caterpillar, *Datana major* Grote & Robinson (Notodontidae) (Williams et al. 1984). This caterpillar can be locally abundant and alarming to growers because of its extensive defoliation to azalea plantings. First stage larvae skeletonize the leaf surface while later stages defoliate the plant.

Grote and Robinson first described adults of *D. major* in 1866. Additional literature concerning adult descriptions was summarized by Packard (1895), and descriptions of the eggs and larvae were summarized by Tietz (1972). Previous descriptions of the egg were brief (Dyar 1890, Packard 1895), and the only photograph illustrated eclosed eggs (Kuitert 1958). We more fully describe uneclosed eggs here.

METHODS

Fourteen eggs were field collected and 20 were obtained from 2 females (10 eggs each) in a laboratory colony at Auburn University maintained on fresh indica azalea cuttings in Percival growth chambers at 30°C light and 24°C dark, with a 14L:10D photoperiod. Eggs were washed in a 1% sodium hypochlorite solution, rinsed in distilled water, air dried, mounted on stubs with double-coated cellophane tape and coated with gold-palladium in a Fullam vacuum sputter coater. External morphology was examined with an ISI-SS40 scanning electron microscope (SEM) using an accelerating voltage of 5 kV. Photographs were taken with Polaroid 55 film. Egg dimensions were recorded by using an ocular micrometer in a stereomicroscope, and egg color was estimated from standard color charts in the Munsell Book of Color (Munsell Color Co. 1976). Color estimates were made under "cool

white" fluorescent overhead lighting. Ultrastructure measurements were made using the SEM. Thirty-four eggs were observed under the SEM.

RESULTS AND DISCUSSION

Eggs of *D. major* are spheroid (Fig. 1), but slightly broadened toward the base. At the broadest point, egg width averaged 1.03 mm (1.00–1.06), and height 0.78 mm (0.76–0.80) (n = 10). Diameter across the top averaged 1.01 mm (1.00–1.06) (n = 10). Although similar in shape and appearance to the eggs of *D. ranaeceps* Guerin-Meneville (Peterson 1963), *D. major* eggs are wider (1.01 mm vs. 0.85 mm) and shorter (0.78 mm vs. 0.85 mm).

The eggs have been described as sublustrous white (Dyar 1890) or uniform white with a large central black spot at the vertex (Packard 1895). When the egg is viewed with the stereomicroscope, the chorion may even appear pearlaceous, a phenomenon which has been observed with other insect eggs (Arbogast & Byrd 1982). When viewed under fluorescent lighting, the eggs appear white to the naked eye, even before eclosion. By comparing eggs with the Munsell Book of Color, a more exact, standard description of the egg is achieved. Eggs were thus estimated to be 2.5 RP 8/2 or No. 2.5 red purple hue, color value No. 8, and chroma No. 2.

The black spot on the vertex mentioned by Packard (1895) is not readily noticeable on newly deposited eggs, but becomes more prominent with embyro development. The caterpillar chews through the chorion in the area of this spot to emerge from the egg. The thickness of the egg shell here is approximately 20 μm. The egg is quite rigid, and resists crushing when pressed between thumb and forefinger. SEM images of eclosed eggs reveal that the egg shell is composed of numerous layers. The innermost layers are densely packed, while outer layers are not as tightly packed, and have larger air spaces.

The chorion surface near the anterior pole forms a rosette-mosaic pattern around a depressed micropylar area (Fig. 2). This area contains three micropyles usually arranged deltoidally (Fig. 3), but sometimes linearly. The micropyles are approximately 2 μm in diameter. Hinton (1981) determined the number of micropyles for 19 species of notodontids but not for the azalea caterpillar. Our finding of three micropyles is the fewest observed to date in this family. The rosette-mosaic pattern on the egg surface represents follicular cell imprints (Margaritis 1985). Each mosaic section is separated by deep grooves bordered by ridges (Fig. 4). These sections may be interconnected by narrow ridges to the surrounding ridges. As the pattern expands from the micropyle, the grooves begin to rise and eventually form only ridges around po-
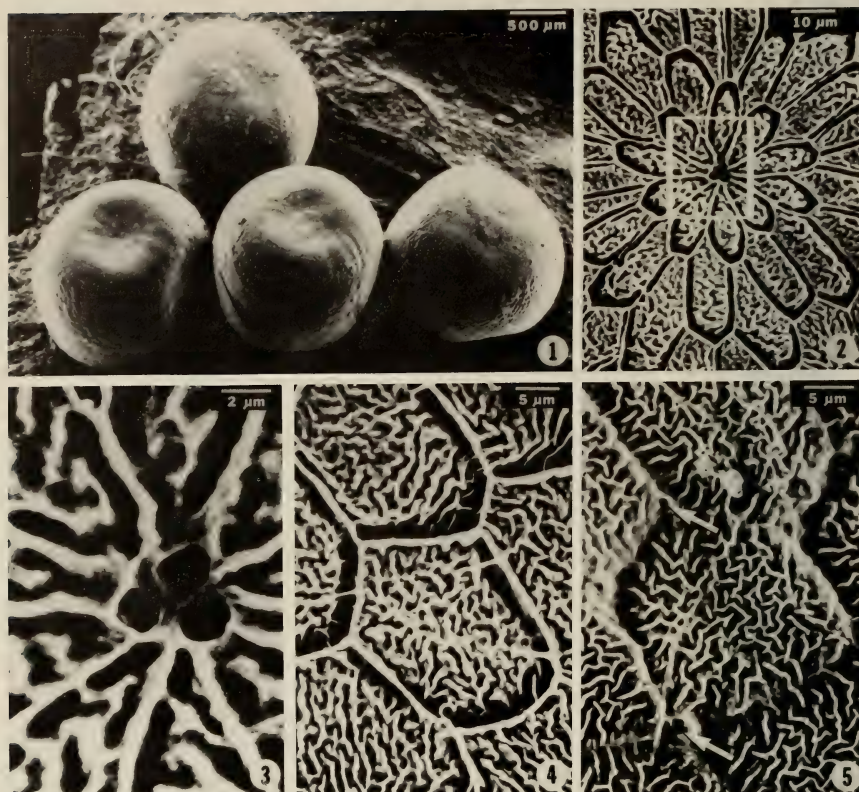
FIGS. 1–5. **1,** Eggs of *Datana major*; **2,** Rosette-mosaic pattern around micropylar area; **3,** Close-up of highlighted micropyles from Fig. 2; **4,** Surface near anterior pole; **5,** Lateral surface of chorion with aeropyles (arrows).

lygonal areas. These polygons are found throughout the surface of the egg. Aeropyles (Fig. 5) are usually found at ridge junctions, and average 1.7 μm (0.7–2.3 μm) (n = 10) in diameter. The polygonous area between these ridges is highly reticulated. The density of aeropyles gradually diminishes toward the micropylar area. No aeropyles were observed in the rosette-mosaic area.

Photomicrographs of the eggs of *D. ranaeceps* (Peterson 1963) resemble those of azalea caterpillar. As with *D. ranaeceps*, *D. major* eggs were firmly attached to each other but could be easily removed from the substrate. We found shell thickness near that of *D. ranaeceps* (20 μm vs. 23 μm). Additionally, SEM images of the aeropyles and surrounding areas of the *D. ranaeceps* egg (Hinton 1981) closely resemble

those of our eggs. However, the number of micropyles differs between *D. ranaeceps* and *D. major* (4 vs. 3).

Datana ranaeceps and *D. major* are obviously similar. Margaritis (1985) concluded that most eggshell features are species-specific, and might prove useful in clarifying phylogenetic and taxonomic problems. As our findings show, comparison of egg chorion morphology could indeed be used to reinforce current classification.

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NEW SPECIES OF OLETHREUTINE MOTHS (TORTRICIDAE) FROM TEXAS AND LOUISIANA

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ABSTRACT. Three new species are described; the male imago and male and female genitalia of each are figured. *Eucosma rosaocellana* is described from eight specimens from northwest Texas, and contrasted with *E. salaciana* Blanchard & Knudson. *Dichrorampha broui* is described from 37 specimens from southeast Louisiana and northeast Texas, and is contrasted with *D. leopardana* (Busck) and *D. incanana* (Clemens). *Pammene medioalbana* is described from nine specimens from central Texas, and is contrasted with *Cydia latiuscula* (Heinrich) and *C. gallaesalaciana* (Riley).

The following three new species of olethreutine moths are described to facilitate completion of a catalogue-checklist of the moths of Texas, a project originated by André Blanchard. Many other undescribed species of Texas Lepidoptera remain or are likely to be discovered in the Tortricidae and other families. In many such cases, the families or their subdivisions are in such great need of revision that isolated descriptions of new species could confuse the situation. Since the last comprehensive revision of *Eucosma* (Heinrich 1923), numerous new *Eucosma* species have been described, but the one described below is quite distinctive, and is closely related to *E. salaciana* Blanchard & Knudson (1981). Heppner (1981) described two new species of *Dichrorampha* from Florida, and Miller (1983) reduced five *Dichrorampha* species names to synonyms, and summarized other recent work in this genus. No new species of *Pammene* have been described from North America since Heinrich's (1926) revision. The holotypes of all species described below are in the U.S. National Museum of Natural History (USNM).

Eucosma rosaocellana E. C. Knudson, new species
(Figs. 1, 4, 7)

Description. *Head:* Front brownish white; vertex pale orange brown; labial palpi porrect, 2nd segment equal to 1½ eye diameter, brownish white dorsally, scale tuft orangish, shading to gray at apex, 3rd segment equal to about ½ eye diameter, brownish white; antennae brownish white, ventral setae about ⅕ width of segments (n = 5). *Thorax:* Orangish brown above, with 3 transverse whitish bands; whitish beneath; legs whitish, tibiae and tarsi with several light gray bands. *Abdomen:* Brownish white above and beneath. *Forewing:* Ratio of length of costal fold (in male) to forewing length 0.32 (n = 5). Ground color whitish, reticulated with irregular vertical bands of grayish brown, and variably suffused with orange brown below costal margin and over lower fold. Subbasal fascia orange brown, margined with blackish brown and weakly represented at costal margin; median fascia grayish brown, margined with blackish brown and weakly represented beyond pretornal spot. Ocelloid patch a trefoil of pinkish opalescent scales

surmounted by a grayish brown patch containing two or three short horizontal black dashes. Costal margin strigulate with about 15 evenly spaced strong blackish brown dashes, with a like number of thinner paler dashes between them, all more or less connected to the irregular vertical bands. Fringe grayish brown mixed with white, mainly white over tornal third. *Hindwing:* Pale grayish brown, paler toward base; darker line at termen and a second dark line at the base of the whitish fringe. *Length of forewing:* Males, 7.1–10.0 mm, average 8.7 mm (n = 7); female, 8.6 mm (n = 1). *Male genitalia* (Fig. 4) (n = 3): Sacculus with ventral margin forming a rounded angle of 105–110 degrees at neck constriction; cucullus broadly rounded at apex, produced ventrally, with many short, spinose setae; cucullus width to length ratio 1.9–2.1; vesica with about 12 deciduous cornuti. *Female genitalia* (Fig. 7) (n = 1): Papillae anales large, bilobed; apophyses anteriores twice as long as apophyses posteriores; lamina postvaginalis well sclerotized, tapering toward an arcuate posterior margin; lamina antevaginalis broad, weakly sclerotized; ductus bursae slightly dilated over middle ⅓, sclerotized on dorsolateral surface, ductus seminalis from just below middle; corpus bursae ovoid, tapering anteriorly, membranous, with two equal sized thornlike signa.

Types. *Holotype* (Fig. 1): Male, Texas, Hemphill Co., Gene Howe Wildlife Management Area, 18-V-85, collected by E. C. Knudson. *Paratypes:* Same data and collector as holotype, 6 males (three with genitalia on slides ECK 1159, 1374, 1375), retained by author; Cottle Co., Matador Wildlife Management Area, 30-VII-83, 1 female (genitalia on slide ECK 1167), in USNM.

Remarks. This species is closely related to *Eucosma salaciana* Blanchard & Knudson (1981), which has a similar forewing pattern, but is marked with dark gray, lacking any trace of orange, and is smaller, with an average forewing length in males of 7.1 mm (n = 28). Male genitalia of the two species are very similar, but the length/width ratio of the cucullus in *salaciana* is 2.2–2.4, and the ventral angle of the sacculus is 90 degrees (n = 4). Female genitalia of *E. salaciana* differ in the lamina postvaginalis, which is bilobed posteriorly, and in the apophyses posteriores, which are one-third the length of the apophyses anteriores (n = 2). The name of the new species refers to the pinkish ocelloid patch.

Dichrorampha broui E. C. Knudson, new species
(Figs. 2, 5, 8)

Description. *Head:* Front and vertex gray; labial palpi exceeding front by 2 eye diameters, dark gray with an oblique whitish band on lateral surface of 2nd segment; antennae gray. *Thorax:* Gray above, paler beneath; legs whitish, tibiae and tarsi banded with gray and white. *Abdomen:* Shiny yellowish gray above and beneath. *Forewing:* Male without costal fold. Ground color grayish white, marked with numerous closely spaced blackish strigulations, outwardly oblique from dorsal margin to radial vein, from there angled inwardly to costal margin. Basal and median fasciae weakly indicated by stronger, darker strigulations. Before termen at middle are three short black horizontal dashes, at tornus, a black dot separated from the three dashes by a whitish patch. Termen slightly produced at apex. On distal half of costal margin are five equally spaced white spots, the inner two or three geminate. Terminal line dark gray; fringe shining yellowish gray. *Hindwing:* Light gray, darker near termen; terminal line dark gray; fringe shining yellowish gray. *Length of forewing:* Males, 5.2–6.0 mm, average 5.5 mm (n = 10); females, 4.9–6.1 mm, average 5.6 mm (n = 10). *Male genitalia* (Fig. 5) (n = 4): Valva with costa bent anteriorly; neck incurvation broad, tapering to a narrow constriction before cucullus; cucullus ovoid, entirely anterior and extending well basad of neck in-
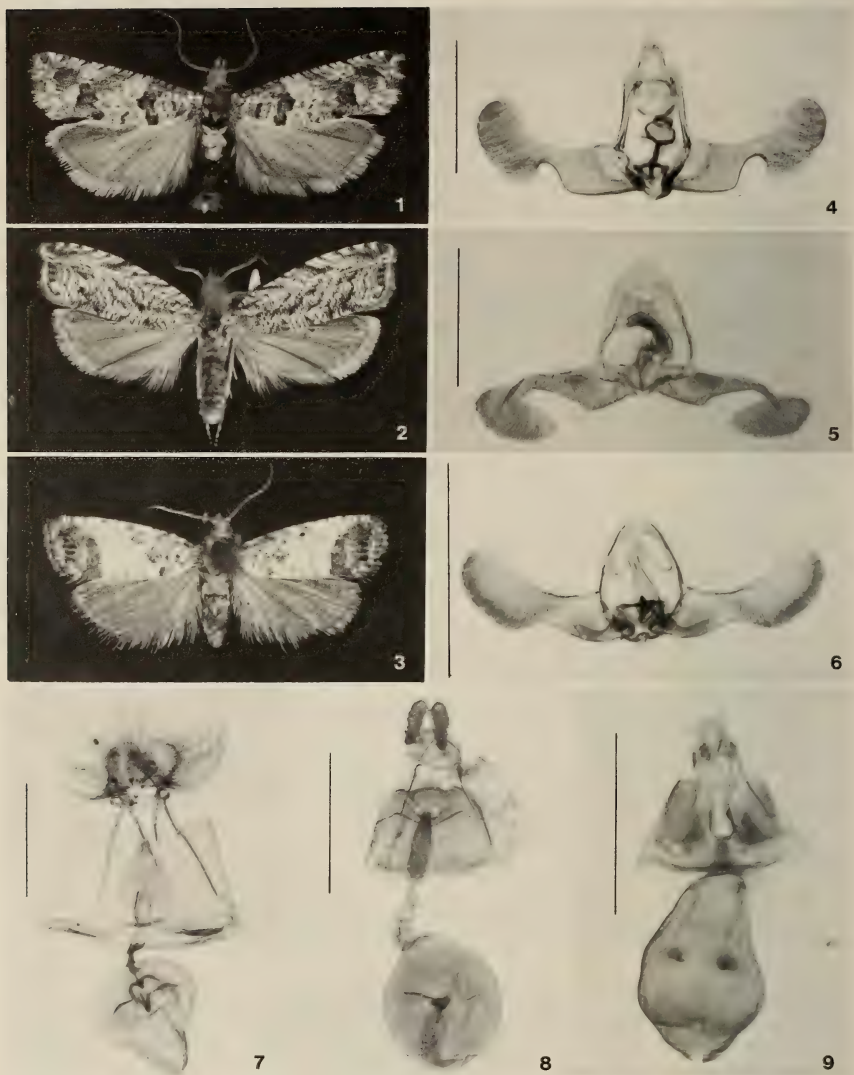
FIGS. 1, 4, 7.   *Eucosma rosaocellana*. **1,** Holotype male; **4,** Male genitalia; **7,** Female genitalia.

FIGS. 2, 5, 8.   *Dichrorampha broui*. **2,** Holotype male; **5,** Male genitalia; **8,** Female genitalia.

FIGS. 3, 6, 9.   *Pammene medioalbana*. **3,** Holotype male; **6,** Male genitalia; **9,** Female genitalia.

Scale lines represent 1 mm.

sertion; vesica with numerous tiny deciduous cornuti. *Female genitalia* (Fig. 8) (n = 2): Apophyses posteriores ⅔ the length of apophyses anteriores; ostium bursae sclerotized, bilobed, with a short median groove; ductus bursae sclerotized over posterior half, ductus seminalis from near middle of anterior half; corpus bursae membranous with 1 thornlike signum.

Types. *Holotype* (Fig. 2): Male, Louisiana, St. Tammany Parish, 4.2 miles (6.7 km) NE Abita Springs, 12-IV-85, collected by V. A. Brou. *Paratypes:* Same locality and collector as holotype, 20-IV-84, 1 male, 1 female; 21-IV-84, 2 females; 22-IV-84, 1 male, 1 female; 29-IV-84, 1 female; 2-V-84, 1 female; 3-V-84, 1 male (genitalia on slide USNM 25933 by J. F. Gates Clarke in USNM); 7-IV-85, 1 female; 12-IV-85, 4 males, 2 females; 13-IV-85, 1 male, 1 female; 18-IV-85, 1 male (genitalia on slide ECK 1302); 19-IV-85, 2 males (one with genitalia on slide ECK 1378), 1 female; 20-IV-85, 4 males, 1 female; 23-IV-85, 1 male; 24-IV-85, 1 female; 27-IV-85, 1 female; all collected by V. A. Brou. Texas, Morris Co., Daingerfield State Park, 22-IV-85, 1 male (genitalia on slide ECK 1136), 1 female (genitalia on slide WEM 25852 by W. E. Miller); Jasper Co., Martin Dies Jr. State Park, 27-IV-86, 2 males, 2 females (one with genitalia on slide ECK 1384), collected by E. C. Knudson. Four Louisiana paratypes in USNM; four retained by author; remainder retained by collector. One Texas paratype in USNM, remainder retained by author.

Remarks. This species is similar in both male and female genitalia to *Dichrorampha leopardana* (Busck) (as illustrated by Heinrich 1926), but *broui* can easily be distinguished by forewing pattern, which lacks the orange striping of *leopardana*. Male genitalia of *D. broui* are also similar to those of *D. incanana* (Clemens) (as represented by Heinrich 1926), but in that species the male has a costal fold. The new species is named for its discoverer, Vernon A. Brou.

Pammene medioalbana E. C. Knudson, new species
(Figs. 3, 6, 9)

Description. *Head:* Front and vertex light gray; labial palpi light gray, exceeding front by ½ eye diameter; antennae dark gray. *Thorax:* Above, anterior ⅔ dark gray, posterior ⅓ whitish; whitish beneath; legs whitish, tarsi faintly banded with light gray. *Abdomen:* Whitish gray above and beneath; male with specialized sex scales on 6th and 7th terga, consisting of 5 or 6 irregular rows of persistent scale tufts on 6th tergum, and 2 or 3 rows of weak scale tufts on 7th tergum; both obscured by superficial scaling. *Forewing:* Ground color white; basal ⅓ suffused with dark brown scales, forming a dark basal patch; median area mainly white with 3 obscure, darker, oblique striations; subterminal area from dorsal margin ¾ the distance from base to just before apex dark brown with a faint coppery luster, enclosing 4 or 5 short, horizontal black dashes margined by narrow silvery metallic bars; costal margin whitish with short, dark brown strigulations, most distinct over apical ⅓; terminal line black, fringe shining gray. *Hindwing:* Dark gray, fringe light gray. *Length of forewing:* Males, 4.0–4.2 mm, average 4.1 mm (n = 6); females, 4.2–4.4 mm, average 4.3 mm (n = 3). *Male genitalia* (Fig. 6) (n = 3): Sacculus with a few strong hairlike setae before slight neck incurvation; cucullus broadly rounded; vesica with 3 or 4 small spinelike nondeciduous cornuti at apex, arranged in a line. *Female genitalia* (Fig. 9) (n = 2): Apophyses posteriores very slender, equal in length to broader apophyses anteriores; ostium bursae a short membranous funnel, lamina postvaginalis well sclerotized, U-shaped; ductus bursae short, well sclerotized; corpus bursae membranous with two small thornlike signa.

Types. *Holotype* (Fig. 3): Male, Texas, Gonzalez Co., Palmetto State Park, 23-III-85, collected by E. C. Knudson. *Paratypes:* Same data and collector as holotype, 5 males (3 with genitalia on slides ECK 1122, 1267, and 1273), 3 females (2 with genitalia on slides ECK 1163 and 1385). One male and one female paratype in USNM, others retained by author.

Remarks. This species is more similar in forewing pattern to *Cydia lautiuscula* (Heinrich 1926) (illustrated by Miller 1976) and *C. gallae-salaciana* (Riley) (as represented by Heinrich 1926) than to other North American species of *Pammene*, but the wing venation, abdominal scale tufts, and male and female genitalia are characteristic of the latter genus.

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RESURRECTION OF *CATASTEGA* CLEMENS AND REVISION OF THE *EPINOTIA VERTUMNANA* (ZELLER) SPECIES-GROUP (TORTRICIDAE: OLETHREUTINAE)

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ABSTRACT. *Catastega* is recognized as a valid genus; *C. timidella*, the type species, and *C. aceriella* are resurrected from synonymy with *Epinotia*; and *E. marmoreana* is transferred to *Catastega*. In the *Epinotia vertumnana* species-group revision, *E. atristriga* is synonymized with *E. zandana*, and *Paedisca celtisana* is synonymized with *E. laracana*. The previously misidentified *E. laracana* is described as a new species. Lectotypes are designated for *Grapholitha subnisana*, a junior synonym of *C. aceriella*, and *Paedisca vertumnana*, which has been previously misidentified as *E. zandana*. Imagos and female genitalia of *Catastega* species are illustrated; imagos and male and female genitalia of six species in the *E. vertumnana* species group are described and illustrated.

The treatment of North American *Epinotia* Hübner by Heinrich (1923) included two species groups with similarly developed male genitalia, both having plesiomorphic forms of an uncus and valva. *Epinotia vertumnana* (Zeller) and five related species comprise the most generalized species-group of the genus, whereas the *E. aceriella* species-group does not appear congeneric with the former. Although a systematic study of world *Epinotia* is near completion, these two species-groups are treated here to clarify nomenclature and make names available to other workers.

For species descriptions, specimens and genitalia were examined with a phase-contrast microscope and stereomicroscope with ocular micrometer, which was used for all measurements. Measurements of forewings are accurate to 0.1; other measurements are accurate to 0.01. The forewing length (FWL) was measured from base to apex, including fringe. The length of sacculus was measured as a straight line from ventral base of valva to beginning of the cucullus, as restricted to the apical portion of the valva with subparallel dorsal and ventral margins (Fig. 8). The number of deciduous cornuti in the aedeagus was obtained by counting their sockets, which were usually distinct. For scanning electron microscopy, specimens were coated with gold-palladium for six min and examined with a Hitachi HH-S-2R scanning electron microscope.

Partial synonymies are given for *Catastega* species to include previous binomial combinations and major references with illustrations of life stages. Complete synonymies are given for species in the *E. vertumnana* group. Specimens in collections of the following individuals and institutions were examined: André Blanchard (AB), American Mu-

seum of Natural History (AMNH), Academy of Natural Sciences, Philadelphia (ANSP), Bryant Mather (BM), British Museum of Natural History (BMNH), Canadian National Collection (CNC), Cornell University (CU), Edward C. Knudson (ECK), Illinois Natural History Survey (INHS), John G. Franclemont (JGF), J. Richard Heitzman (JRH), Kansas State University (KSU), Natural History Museum of Los Angeles (LACM), Museum of Comparative Zoology (MCZ), Mississippi Entomological Museum (MEM), Michigan State University (MSU), Richard L. Brown (RLB), University of California, Berkeley (UCB), United States National Museum of Natural History (USNM). Label data from these specimens have been recorded and deposited in the Mississippi Entomological Museum.

RESURRECTION OF *CATASTEGA*

In 1862 Brackenridge Clemens erected the genus *Catastega* for *aceriella* and *timidella*, based solely on larval habits. Larvae incorporate frass with silk to form serpentine tubes on the underside of leaves (Fig. 1), similar to some Gelechiidae and Pyralidae. The tubes and feeding area are covered by a loose web of silk, which causes the leaf to crumple as larvae mature. The family placement was uncertain until H. G. Dyar reared an adult of *C. timidella*, which was determined to be a tortricid (Busck 1903). Heinrich (1923) treated *Catastega* as a synonym of *Epinotia* and described *E. marmoreana*, which is transferred to *Catastega* here.

Catastega is characterized as follows: forewing usually with well developed pretornal triangular spot, often with reticulations between fascia, costal strigulae present or absent, male costal fold present or absent; male genitalia with uncus bifid, socii broad, setose, ventrally fused with bases of gnathos, anellus not closely surrounding base of aedeagus, often cuplike, valva with saccular spine cluster, cucullus poorly defined or delimited by deep ventral invagination; female with lamella postvaginalis reduced, lamella antevaginalis developed and forming conelike sterigma around ostium, ductus bursae with sclerotized band posterior to inception of ductus seminalis, two signa present.

The previous inclusion of *Catastega* with *Epinotia* was based on plesiomorphic characters that also are present in some Olethreutini, such as *Omiostola* Meyrick: uncus well developed and bifid, socius broadly joining tegumen, valva with a saccular spine cluster. The male anellus and female sterigma are apomorphic for *Catastega*.

Although *Catastega* is known to occur only in North America, the genus appears to be closely related to *Pseudacroclita* Oku, which is endemic to Japan. Larvae of the latter genus also spin a tubular nest
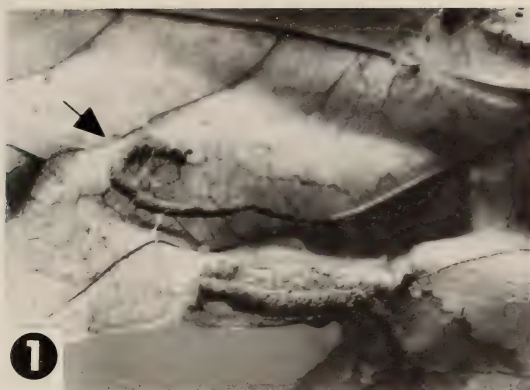
FIG. 1.   Larval feeding tube (arrow) of *Catastega aceriella* on *Acer* sp., Ithaca, New York.

covered by a sparse web on the lower surface of leaves. Female genitalia of the type species, *P. hapalaspis* (Meyrick), are very similar to *Catastega* species, but the male differs in having a short, broad uncus, and a different form of aedeagus and valva (Oku 1979).

Catastega Clemens, revised status

Catastega Clemens (1861 [1862]:86). Type species: *Catastega timidella* Clemens, by
    subsequent designation (Busck 1903:852).

Catastega aceriella Clemens, revised status
(Figs. 2, 5)

Catastega aceriella Clemens (1861 [1862]:86).
Hedya signatana Clemens (1864 [1865]:514); Miller (1973:222, fig. 41, imago).
Steganoptycha variana Clemens (1864 [1865]:520); Miller (1973:224, fig. 49, imago).
Grapholitha subnisana Zeller (1875:294).
Semasia signatana; Fernald (1902 [1903]:462); Felt (1905:168, fig. 24, larval work); Mosher (1916:54).
Gelechia aceriella; Busck (1902 [1903]:515).
Enarmonia aceriella; Fernald (1908:39, 56).
Eucosma sigmatana Barnes & McDunnough (1917:172, misspelling).
Epinotia aceriella; Heinrich (1923:244, fig. 372, ♂ genitalia); MacKay (1959:118, fig. 111, larva), (1962:638); Miller (1973:211); Côté & Allen (1973:463–470, figs. 3–9, egg, larval work, pupa, imago); Johnson & Lyon (1976:178, Pl. 81, figs. a–c, larval work).

Types. *aceriella* description based on larval work; type locality: unknown locality in North America. *signatana*—Holotype, ♂, in ANSP; type locality: Virginia. *variana*—Lectotype, ♀, designated by Miller (1973); in ANSP; type locality: Maine or Easton, Pennsylvania. *subnisana*—Lectotype here designated, ♂, "Mass.-Maine? Packard" [green label], genitalia slide BM No. 11597; a lectotype label was previously affixed to the specimen by N. S. Obraztsov, but no formal designation was published; a lectotype label dated 1986 with designation by R. L. Brown has been added to the specimen; in BMNH; type locality: "Maine-Mass.?".

Figs. 2–4.   Imagos of *Catastega* species. **2,** *C. aceriella,* male, Tompkins Co., New York; **3,** *C. marmoreana,* female, Coconino Co., Arizona; **4,** *C. timidella,* male, Tompkins Co., New York.

Distribution. Eastern North America from S Ontario and Nova Scotia to North Carolina and Tennessee, W to Illinois and Minnesota.
Hosts. *Acer* spp.
Material examined. Types of *signatana, variana, subnisana*; 91 ♂, 36 ♀ (AMNH, ANSP, BMNH, CNC, CU, INHS, JGF, RLB, UCB, USNM).

Catastega marmoreana Heinrich, new combination
(Figs. 3, 6)

Epinotia marmoreana Heinrich (1923:222, fig. 349, ♂ genitalia).

Type. Holotype, ♂, USNM Type No. 24852, genitalia slide "CH 2 Nov. 1920"; in USNM. Type locality: Stockton, Utah.
Distribution. Western United States from N Arizona and New Mexico to S Wyoming.
Host. Unknown.
Material examined. ♂ Type, 15 ♂, 29 ♀ (AMNH, INHS, JGF, LACM, USNM).

Catastega timidella Clemens, revised status
(Figs. 4, 7)

Catastega timidella Clemens (1861 [1862]:96).
Gelechia timidella; Busck (1902 [1903]:518).
Enarmonia timidella; Fernald (1908:39).
Epinotia timidella; Heinrich (1923:223, fig. 373, ♂ genitalia); MacKay (1962:638, fig. 7, larva); Miller (1973:224).

Type. *timidella* description based on larval work; type locality: St. Paul, Minnesota?
Distribution. Eastern North America from S Canada to Virginia, W to Illinois and Minnesota; British Columbia (probable introduction).
Hosts. *Quercus* spp.
Material examined. 71 ♂, 50 ♀ (AMNH, ANSP, CNC, CU, INHS, JGF, LACM, RLB, UCB, USNM).

Discussion

The three described species are differentiated easily by wing pattern. *Catastega timidella* and *C. aceriella* cannot be separated easily by characters of male genitalia. The female *C. aceriella* has sternum VII without rugae, tergum VIII and papillae anales narrower, and sterigma
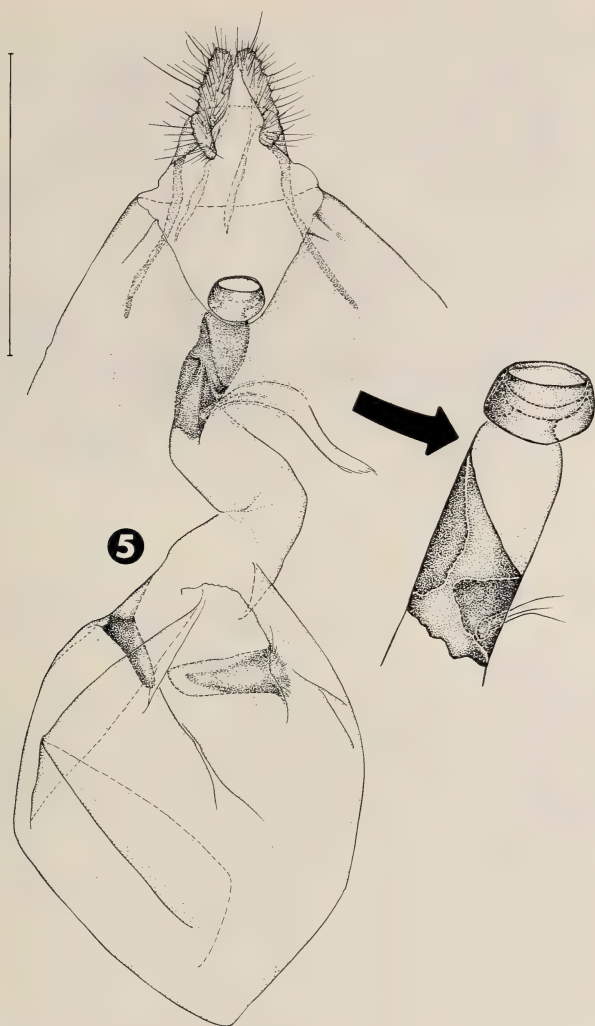
FIG. 5. Female genitalia of *Catastega aceriella*, Pittsburgh, Pennsylvania, USNM slide 17600, with sterigma and ductus bursae enlarged. Scale line = 1 mm.

more rounded than *C. timidella*. Both sexes of the western *C. marmoreana* differ greatly from eastern species, especially in shape of male valva and female sterigma. More than 10 undescribed species occurring in SW United States and Mexico and at least one new species in E United States have been collected recently. These will be described when additional material becomes available; some are represented by only one sex.
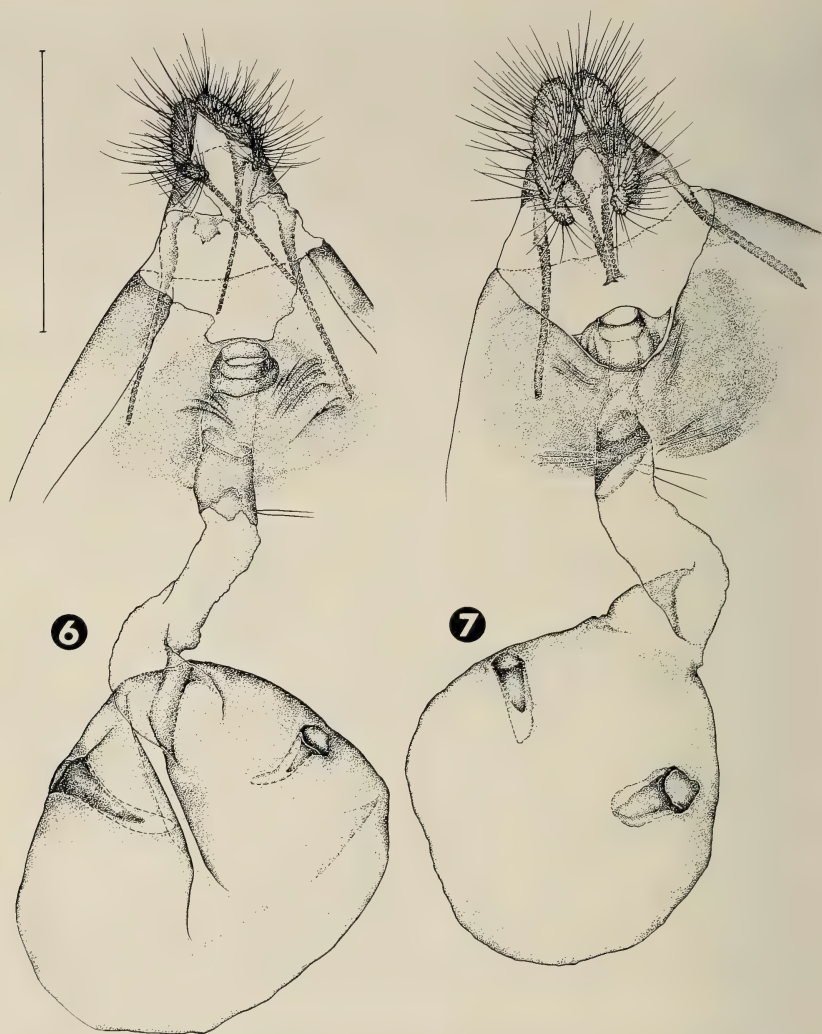
FIGS. 6, 7.   Female genitalia of *Catastega* species. **6,** *C. marmoreana,* Colorado Springs, Colorado, RLB slide 471 (INHS); **7,** *C. timidella,* Aweme, Manitoba, RLB slide 523 (CNC). Scale line = 1 mm.

REVISION OF THE *EPINOTIA VERTUMNANA* SPECIES-GROUP

The *E. vertumnana* species-group of Eucosmini includes six species of grayish brown moths, all of which occur E of the Rocky Mountains in North America. Species in this group are the most difficult to identify among all *Epinotia* because of obscure and variable forewing fasciae in most, and similarity of color pattern and male genitalia among
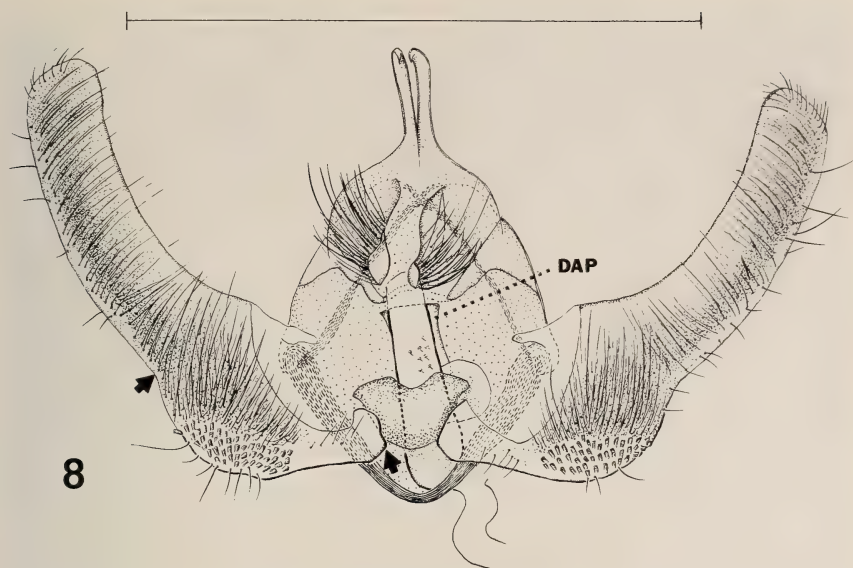
FIG. 8. Male genitalia of *Epinotia vertumnana*, Dallas, Texas, RLB slide 1155 (MCZ). DAP, dorsal anellar plate; length of sacculus measured as straight line between arrows. Scale line = 1 mm.

some. Of the six treated here, five were misidentified in the last revision of North American Eucosmini (Heinrich 1923).

Imagos of this group are among the first tortricids to fly during early spring, and are often collected with *Pseudexentera* and *Chimoptesis*. *Epinotia* can be separated from the latter two genera and other Eucosmini by the following genital characters: in the male, uncus developed, socius arising laterally rather than dorsally from tegumen, gnathos usually not fused medially, anellus usually closely surrounding aedeagus and extended dorsally as an anellar plate; and in the female, sternum VII not fused with sterigma and not posteriorly invaginated around ostium, lamella antevaginalis reduced, and ductus bursae with sclerotized, denticulate band or plate near inception of ductus seminalis.

Species in the *vertumnana* group share the following characters: length of third segment of labial palpus less than half the length of second; scales of head, tegulae, and mesonotum concolorous with forewing ground color; forewing outer margin straight, forming an acute angle with costal margin; male costal fold present or absent, enclosing hair pencils; hindwing light grayish brown, without contrasting colors; in the male, uncus bifid from near base; socius arising from bulbous expansion of tegumen, elongate, apically rounded, setose on dorsal

margin from apex to base of uncus; gnathos arising from tegumen and base of socius, heavily sclerotized basally; aedeagus moderately long and stout; anellus closely surrounding aedeagus basally, divergent apically; caulis of juxta V-shaped in cross-section; valva with well defined saccular spine cluster; cucullus not well defined nor delimited by neck; in the female, sternum VII with medial area more lightly sclerotized than lateral areas, without depressions and microtrichia; tergum VIII setose, without scales; lamella postvaginalis with microtrichia present medially, setose laterally; ductus bursae spiraled, medial sclerotized band encircling ductus bursae much wider on one side than other; two signa present. Species of the *vertumnana* group can be separated easily from other *Epinotia* by the grayish brown forewings with acute apex and poorly defined fasciae, the form of bifid uncus, the valva with a well defined saccular spine cluster and poorly defined cucullus (Fig. 8), and in the female, by the lightly sclerotized medial line of sternum VII and form of the sterigma.

Epinotia zandana (Kearfott)
(Figs. 9, 10, 18, 19, 26)

Eucosma zandana Kearfott (1907:25).
Eucosma peristicta Meyrick (1912:34, invalid replacement name).
Epinotia atristriga Clarke (1953:228). **NEW SYNONYMY.**

Adult. ♂ Types, *zandana*, *atristriga*; 58 ♂, 48 ♀ examined (AMNH, ANSP, CNC, CU, ECK, JRH, INHS, KSU, MSU, RLB, UCB, USNM).
Forewing (Figs. 9, 10). FWL: 6.0–8.5 mm; length of costal fold 0.42–0.46 FWL (12n); most specimens dark grayish brown peppered with variable number of white or white-tipped scales, white scales usually forming a longitudinal sinuate line on inner marginal half; some specimens with narrow, brown, subbasal and median fasciae, median fascia interrupted near CuA1 to form pretornal triangular spot; some specimens with brown, continuous or interrupted, longitudinal streak from base to apex.
Male genitalia (Figs. 18, 19). Width of uncus at bifurcation 0.44–0.48 greatest width of juxta; dorsal anellar plate with straight lateral margins, apically curved outward; aedeagus with 9–11 cornuti (5n); valva abruptly narrowed beyond sacculus, cucullus much longer than sacculus; saccular spine cluster rounded. Twenty-three preparations examined (AMNH, CNC, ECK, MSU, UCB, USNM).
Female genitalia (Fig. 26). Tergum VIII with row of setae on posterior margin, bare medially, anterior margin with rounded medial notch; papillae anales large, with dense setae and microtrichia, facing laterally, subequal in width anteriorly and posteriorly; length of anterior apophyses 1.0–1.1 length of posterior apophyses (7n); posterior margin of sterigma straight to slightly concave; bursa seminalis without spinules; width of posterior signum 1.7–2.7 width of anterior signum (8n). Twenty-one preparations examined (ANSP, CNC, INHS, MSU).
Types. *Eucosma zandana*—Lectotype, ♂, genitalia slide by Klots, 26 Oct. 1941; designated by Klots (1942); in AMNH. Type locality: Cincinnati, Ohio. *Epinotia atristriga*—Holotype, ♂, genitalia slide CH#1, 13 Aug. 1940; in USNM. Type locality: Putnam Co., Illinois. The *zandana* lectotype is similar to the specimen in Fig. 9; the *atristriga* holotype is similar to the specimen in Fig. 10. The *atristriga* holotype is labeled as collected on 24 March 1938, rather than 17 March 1938, as given in error by Clarke (1953). The female genitalia illustrated by Clarke for *atristriga* are those of *E. laracana*.
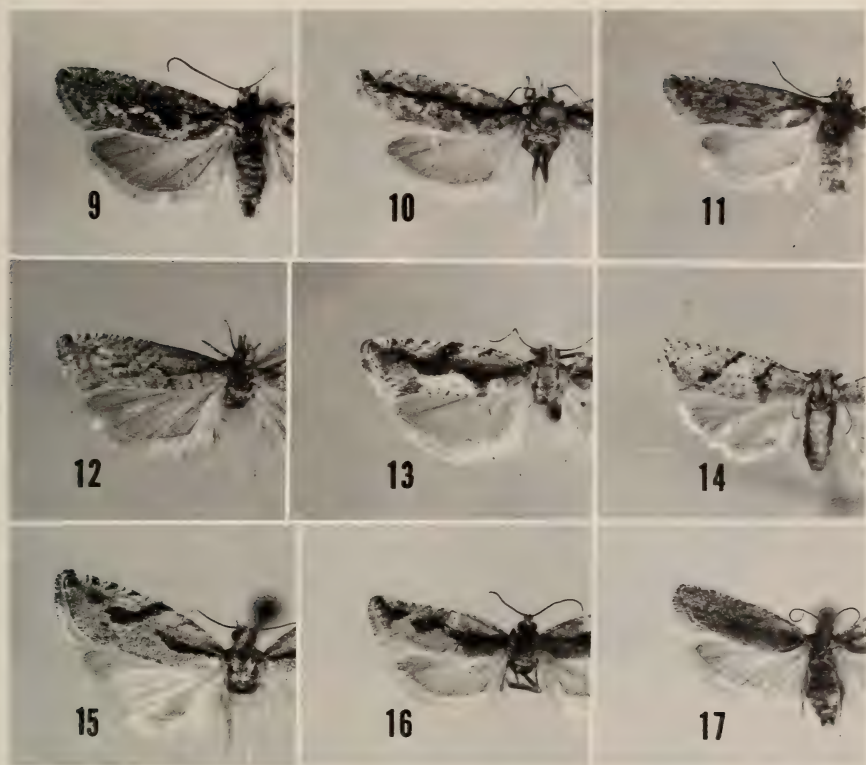
FIGS. 9–17. Imagos of *Epinotia* species. **9,** *E. zandana*, female, no data; **10,** *E. zandana*, male, Ottawa, Ontario; **11,** *E. bicordana*, male, Aweme, Manitoba; **12,** *E. laracana*, male, Dallas, Texas; **13,** *E. laracana*, female, Ottawa, Ontario; **14,** *E. xandana*, female, Cincinnati, Ohio; **15,** *E. sotipena*, female paratype, Ithaca, New York; **16,** *E. vertumnana*, female, Merivale, Ontario; **17,** *E. vertumnana*, female, Clifton Springs, New York.

Geographical distribution and flight times. S Ontario and Quebec (24 Mar.–29 Apr.) to Massachusetts (16 Mar.–1 May), W to Michigan (21 Mar.–13 Apr.), and S to Arkansas (4–13 Mar.) and E Texas (17 Feb.–10 Mar.).

Host. *Crataegus* sp. (one specimen reared by T. N. Freeman in Ontario).

Discussion. Specimens that Heinrich (1923) treated as *E. zandana* are conspecific with the lectotype of *E. vertumnana*. Most specimens of *E. zandana* can be differentiated from other members of the species group by the darker color of the forewings. This species is easily identified by the broad base of uncus, rounded saccular spine cluster of valva, and cucullus that is much longer than the sacculus. The female is distinctive in having broad papillae anales with dense setae and microtrichia, and can be identified without dissection. The short ovipositor (with posterior and anterior apophyses subequal in length) and

the densely setose papillae anales suggest that eggs are not inserted into crevices or buds, in contrast to the inserting form of ovipositor with reduced papillae anales (Figs. 30, 31). The papillae anales of many females have debris packed between setae.

Epinotia bicordana Heinrich
(Figs. 11, 20, 27)

Epinotia bicordana Heinrich (1923:220, fig. 368).

Adult. ♂ Type, 12 ♂, 7 ♀ examined (AMNH, CNC, USNM).
Forewing (Fig. 11). FWL: 6–7 mm; costal fold absent; basal third of costa rolled dorsally and slightly posteriorly; uniformly grayish brown, some specimens with narrow, dark grayish brown subbasal and median fasciae.
Male genitalia (Fig. 20). Width of uncus at bifurcation 0.24 greatest width of juxta (1n); dorsal anellar plate with sinuate lateral margins; aedeagus with six cornuti (1n); valva abruptly narrowed beyond sacculus, cucullus much longer than sacculus; saccular spine cluster elongate. Two preparations examined (AMNH, USNM).
Female genitalia (Fig. 27). Tergum VIII with 1–2 rows of setae on posterior margin, anterior margin W-shaped, median notch acute; papillae anales large, facing ventrally, posterior cleft shallow, subequal in width anteriorly and posteriorly; posterior and anterior apophyses subequal in length; posterior margin of lamella postvaginalis slightly sinuate; bursa seminalis without spinules; width of posterior signum 1.6 width of anterior signum. One preparation examined (CNC).
Type. Holotype, ♂, genitalia slide "#5, Jan. 30, 1920"; in AMNH. Type locality: Aweme, Manitoba.
Geographical distribution and flight times. Known only from Aweme, Manitoba (26 Mar.–27 Apr.).
Host. Unknown.

Discussion. This species is superficially similar to uniformly colored individuals of *E. zandana* and *E. vertumnana*. Males of *E. bicordana* differ from males of all related species in lacking a forewing costal fold. The female can be easily identified by the combination of the W-shaped anterior margin of tergum VIII, and the broad, ventrally facing papillae anales. Debris was absent on the papillae anales of the single female examined.

Epinotia xandana (Kearfott)
(Figs. 14, 21, 28)

Paedisca vertumnana; Zeller (1875:310, part, var. c).
Eucosma xandana Kearfott (1907:24).
Eucosma atacta Meyrick (1912:34, invalid replacement name).

←

FIGS. 18–25. Male genitalia of *Epinotia* species. **18**, *E. zandana*, Putnam Co., Illinois, JFGC 10564 (USNM); **19**, *E. zandana*, Cincinnati, Ohio, Klots 26 Oct. 1941, lectotype (AMNH); **20**, *E. bicordana*, Aweme, Manitoba, USNM 17668; **21**, *E. xandana*, New Brighton, Pennsylvania, CH 8 Oct. 1924 (USNM); **22**, *E. vertumnana*, Merivale, Ontario, RLB slide 569 (CNC); **23**, *E. sotipena*, Cincinnati, Ohio, RLB slide 575 (ANSP); **24**, *E. laracana*, Dallas, Texas, RLB slide 573 (MCZ); **25**, *E. laracana*, Cincinnati, Ohio, USNM slide 17719.
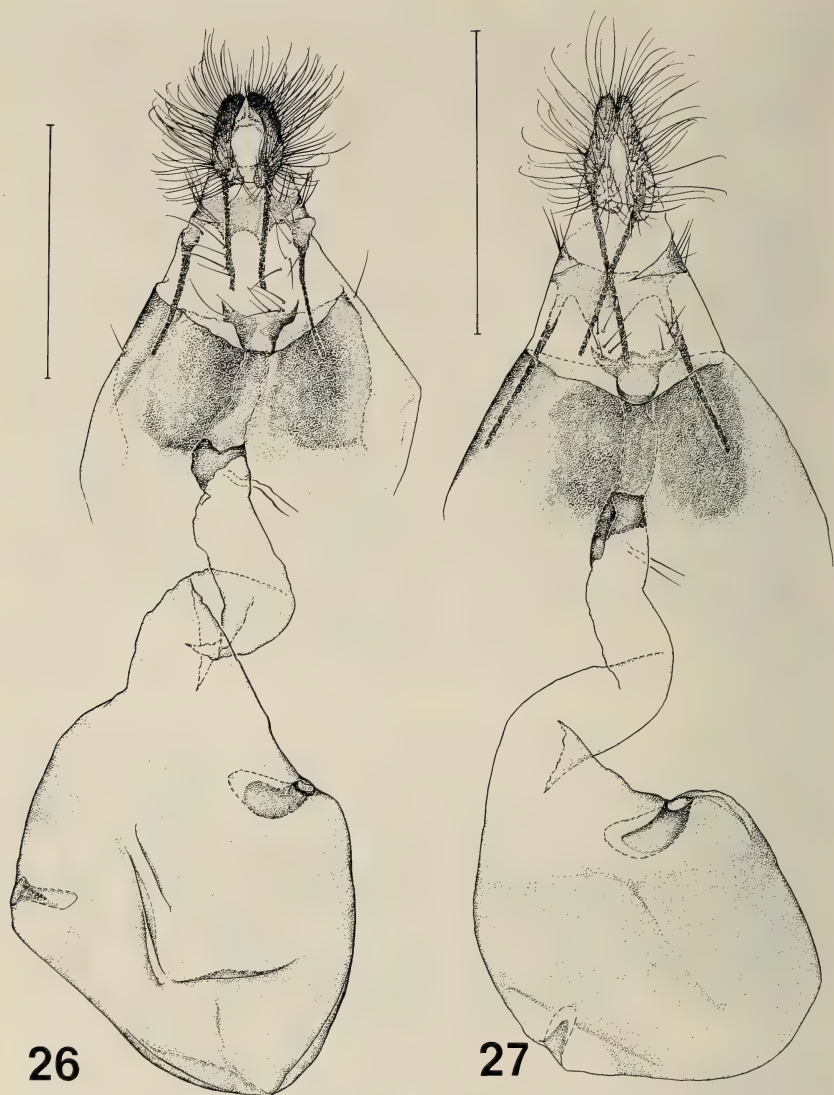
FIGS. 26, 27.   Female genitalia of *Epinotia* species. **26,** *E. zandana*, Cincinnati, Ohio, RLB slide 453 (ANSP); **27,** *E. bicordana*, Aweme, Manitoba, RLB slide 552 (CNC). Scale lines = 1 mm.

Epinotia xandana; Heinrich (1923:204, as synonym of *vertumnana*), (1929:15).
Eucosma yandana Kearfott (1907:25).
Eucosma nothrodes Meyrick (1912:34, invalid replacement name).
Epinotia yandana; Heinrich (1923:206, fig. 369), (1929:15, as synonym of *xandana*).

Adult. ♂ Types, *xandana*, *yandana*; 15 ♂, 18 ♀ examined (AB, ANSP, JRH, RLB, CNC, LACM, MEM, USNM).
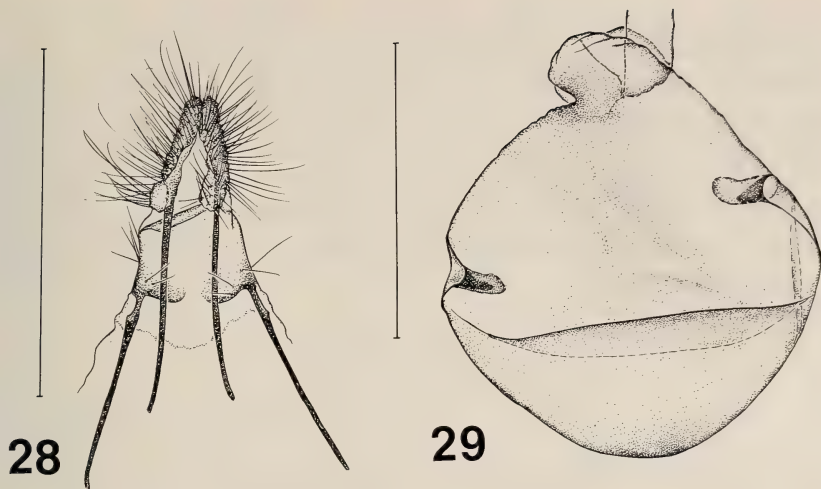
FIGS. 28, 29.   Female genitalia of *Epinotia* species. **28,** *E. xandana,* eighth segment and papillae anales, Cincinnati, Ohio, RLB slide 462 (CNC); **29,** *E. laracana,* corpus bursae, Dallas, Texas, RLB slide 458 (MCZ).

Forewing (Fig. 14). FWL: 6.0–8.0 mm; length of costal fold 0.33–0.38 FWL (5n); grayish white or dark grayish brown with brown subbasal and median fasciae, some specimens with scattered brown scales forming reticulations between fascia.

Male genitalia (Fig. 21). Width of uncus at bifurcation 0.25–0.27 greatest width of juxta (2n); dorsal anellar plate with straight to slightly sinuate lateral margins, not expanded apically; aedeagus with eight cornuti (1n); valva abruptly narrowed beyond sacculus; saccular spine cluster elongate. Five preparations examined (ANSP, RLB, USNM).

Female genitalia (Fig. 28). Tergum VIII sclerotized laterally, forming two narrow tergites, with irregular row of setae on posterior margins of tergites, anterior margin of each tergite straight, forming acute angle with anterior apophyses; papillae anales as in *bicordana,* except slightly less setose; length of anterior apophyses 0.88–0.97 length of posterior apophyses (4n); posterior margin of sterigma concave; seminalis bursae without spinules; width of posterior signum 2.0–2.2 width of anterior signum (3n). Six preparations examined (ANSP, CNC, RLB, USNM).

Types. *Eucosma xandana*—Lectotype, ♂, genitalia CH 15 Dec. 1919. Type locality: Cincinnati, Ohio. *Eucosma yandana*—Lectotype, ♂, genitalia slide "CH June 17, 1924". Type locality: New Brighton, Pennsylvania. Both lectotypes designated by Klots (1942); in AMNH.

Geographical distribution and flight times. Western Pennsylvania and Ohio (3 Mar.–12 Apr.) to N Mississippi (21–24 Feb.), and E Texas (27 Feb.).

Host. Unknown.

Discussion. The grayish white forewing was thought to distinguish this species from all others. Dark specimens recently collected with grayish white specimens in Mississippi are similar in fasciae, reticulated lines between fasciae, length of forewing costal fold, and in male and female genitalia. A uniformly dark female in poor condition is among the co-types of Zeller's *Paedisca vertumnana,* and the partially damaged genitalia suggest it should be assigned to this species. These dark specimens indicate a degree of variation similar to that in related species;

this species differs from others in having a light form with transverse
fasciae rather than a longitudinal dark streak. The female is similar to
E. zandana and *E. bicordana* in having papillae anales that are not
reduced, and posterior and anterior apophyses that are subequal in
length; it resembles *E. vertumnana*, *E. laracana*, and *E. sotipena* in
having the tergum reduced to lateral tergites. The papillae anales of
some females are covered with debris, similar to *E. zandana*. The male
genitalia are similar to those of *E. vertumnana*, but differ in having a
narrower uncus, a dorsal anellar plate not expanded apically, and a
wider saccular spine cluster.

Epinotia laracana (Kearfott)
(Figs. 12, 13, 24, 25, 29)

Proteopteryx laracana Kearfott (1907:45).
Proteopteryx navalis Meyrick (1912:34, invalid replacement name).
Paedisca vertumnana Zeller (1875:310, part, var. e, f).
Epinotia vertumnana; Heinrich (1923:204, part, inc. fig. 371).
Epinotia atristriga; Clarke (1953:228, part, fig. 3b).
Paedisca celtisana Riley (1881 [1882]:319); Fernald (1902 [1903]:459, as *Eucosma*); Heinrich (1923:204, as synonym of *vertumnana*). **REVISED SYNONYMY.**

Adult. ♀ Type *laracana*, ♂ type, *celtisana*; 22 ♂, 48 ♀ examined (AMNH, ANSP, CNC, ECK, INHS, MCZ, MEM, MSU, RLB, USNM).
Forewing (Figs. 12, 13). FWL: 6.1–7.2 mm; length of costal fold 0.39–0.45 FWL (20n); light grayish brown to grayish brown intermixed with variable amounts of white or white-tipped scales; narrow to broad brown subbasal fascia extending from middle of discal cell to inner margin; narrow to broad brown median fascia usually extending from costa to CuA1, usually widened in discal cell; brown preapical and apical spots present or absent; most specimens with longitudinal streak between wing base and basal fascia, some specimens with sinuate, longitudinal streak between wing base and basal fascia, some specimens with sinuate, longitudinal streak extending from base through subbasal and median fasciae to preapical spot, some longitudinally streaked specimens with large, white spot at middle of inner margin (Fig. 13); some specimens suffused with grayish orange between median fascia and apex.
Male genitalia (Figs. 24, 25). Width of uncus at bifurcation 0.26–0.35 width of juxta; dorsal anellar plate with sinuate lateral margins; aedeagus with 14–17 cornuti (13n); valva tapered or narrowed near middle, length of cucullus less than or subequal length of sacculus; saccular spine cluster elongate. Thirty-seven preparations examined (AMNH, CNC, ECK, MCZ, MSU, MEM, RLB, USNM).
Female genitalia (Fig. 29). Tergum VIII as in *xandana*; papillae anales reduced, posterior half facing ventrally, anteriorly narrowed and facing laterally; length of anterior apophyses 0.70–0.79 length of posterior apophyses (28n); posterior margin of lamella postvaginalis V-shaped, acutely angled; bursa seminalis with sparse, small spinules; width of posterior signum 1.0–1.4 width of anterior signum (25n). Thirty-two preparations examined (AMNH, BM, CNC, ECK, MCZ, MSU, USNM).
Types. *Proteopteryx laracana*—Lectotype, ♀, designated by Klots (1942); in AMNH. Type locality: Cincinnati, Ohio. *Paedisca celtisana*—Holotype, ♂, in USNM. Type locality: Dallas, Texas. *E. laracana* was described from 13 specimens, 8 of which are *E. vertumnana*.
Geographical distribution and flight times. Southern Ontario (26 Apr.) to E Pennsylvania (19 Apr.), W to Wisconsin (20 May), and S to central Mississippi (8 Mar.) and E Texas (10 Feb.).
Host. *Celtis* (holotype of *celtisana*).

Discussion. Identities of *E. laracana*, *E. vertumnana*, and a new species, *E. sotipena*, have been confused frequently. Males of *E. laracana* can be identified by characters including forewing maculation (Figs. 12, 13), more tapered valva, aedeagus with 14–17 cornuti (more than any related species), and dorsal anellar plate with sinuate lateral margins. Females are distinctive among related species in having signa subequal in width. *E. laracana* appears to have a flight period concurrent with *E. sotipena*, and slightly later in the spring than *E. vertumnana*.

Epinotia sotipena Brown, new species
(Figs. 15, 23, 31)

Proteopteryx laracana Kearfott (1907:45, part).
Epinotia laracana; Heinrich (1923:204).

Adult. 21 ♂, 45 ♀ examined (AMNH, ANSP, CNC, CU, INHS, JGF, JRH, RLB, USNM).
Forewing (Fig. 15). FWL: 5.8–8.2 mm; length of male costal fold 0.31–0.35 FWL (15n); light grayish brown intermixed with variable amounts of white or white-tipped scales; brown basal streak extending from base to 0.39–0.45 FWL; curved, brown, median fascia extending from costa to CuA1; brown preapical spot present or absent, confluent with median fascia in some specimens; small, brown apical spot present or absent, confluent with preapical spot in some specimens, strigulae on basal third and apical third of costa, basal row of outer marginal scales, and scattered scales in tornus dark grayish brown, most specimens suffused with grayish orange between median fascia and apex, some specimens also suffused with grayish orange between base and median fascia.
Male genitalia (Fig. 23). Width of uncus at bifurcation 0.24–0.30 greatest width of juxta; dorsal anellar plate and valva as in *laracana*; aedeagus with 12–14 cornuti; saccular spine cluster elongate. Nine preparations examined (ANSP, CNC, INHS, JGF, USNM).
Female genitalia (Fig. 31). Tergum VIII as in *E. xandana*, except lateral tergites narrowed medially, anterior margin of each tergite forming obtuse angle with anterior apophyses; papillae anales as in *E. laracana*; length of anterior apophyses 0.60–0.69 length of posterior apophyses; lamella postvaginalis as in *E. laracana*; bursa seminalis with dense, large spinules; width of posterior signum 2.0–3.3 width of anterior signum (5n). Nine preparations examined (CNC, INHS, USNM).
Holotype. ♀, Plummers Id. [Island], Md. [Montgomery Co., Maryland], 7-IV-62, R. W. Hodges. U.S.N.M. Type No. 76280; in USNM. Data given as on the label except for bracketed information. Specimen is not dissected, is in excellent condition, and has a forewing length of 7 mm.
Paratypes. *Arkansas:* Johnson Co., 9 mi [14.5 km] N Clarksville, 11 Mar. 1985, R. L. Brown (1 ♂, genit. slide RLB 1425). *Illinois:* Putnam Co., 1 May 1937 (1 ♀, genit. slide USNM 17718), 2 Apr. 1939 (1 ♂, genit. slide RLB 446), 5 Apr. 1939 (1 ♂, genit. slide CH 13 Aug. 1940, #3), 9 Apr. 1939 (1 ♀), 14 Apr. 1940 (1 ♂), 21 Apr. 1940 (1 ♀, genit. slide RLB 456), 28 Mar. 1943 (1 ♀, genit. slide RLB 166). *Maryland:* same data as Holotype (2 ♂, 2 ♀, ♀ genit. slide USNM 17674). *Missouri:* Jackson Co., Independence, 12 Apr. 1969, J. R. Heitzman (1 ♂), Kansas City, 13 Apr. 1969 (1 ♂); Jasper Co., Sarcoxie, city limits, open field, 15 Apr. 1975, R. Letsinger (1 ♀). *New York:* Tompkins Co., Ithaca, Six Mile Creek, 20 Apr. 1957, J. G. Franclemont (1 ♂, 1 ♀, ♂ genit. slide JGF 4478), 22 Apr. 1957 (1 ♂), 24 Apr. 1957 (1 ♂, 1 ♀), 26 Apr. 1957 (1 ♀), 25 Apr. 1959 (2 ♂, 3 ♀, ♂ genit. slide RLB 576), 16 Apr. 1960 (1 ♀), 7 May 1961 (1 ♀), same data except R. W. Hodges, 18 Apr. 1959 (1 ♀), 27 Apr. 1961 (1 ♀, genit. slide USNM 17617), 7 May 1961 (1 ♂, 3 ♀), 12 May 1961 (1 ♀), Buttermilk Falls, Apr. 1920 (1 ♂). *Ohio:* Hamilton Co, Cincinnati, 19 Mar. 1903, Annette F. Braun (2 ♀, genit. slide CNC Epi. 12), 26 Mar. 1903 (1 ♀), 15 Apr. 1904 (1 ♀), 17 Mar. 1905 (1 ♂, genit. slide CNC 12), 3 Apr. 1906 (2 ♂, 9 ♀), 20 Mar. 1904
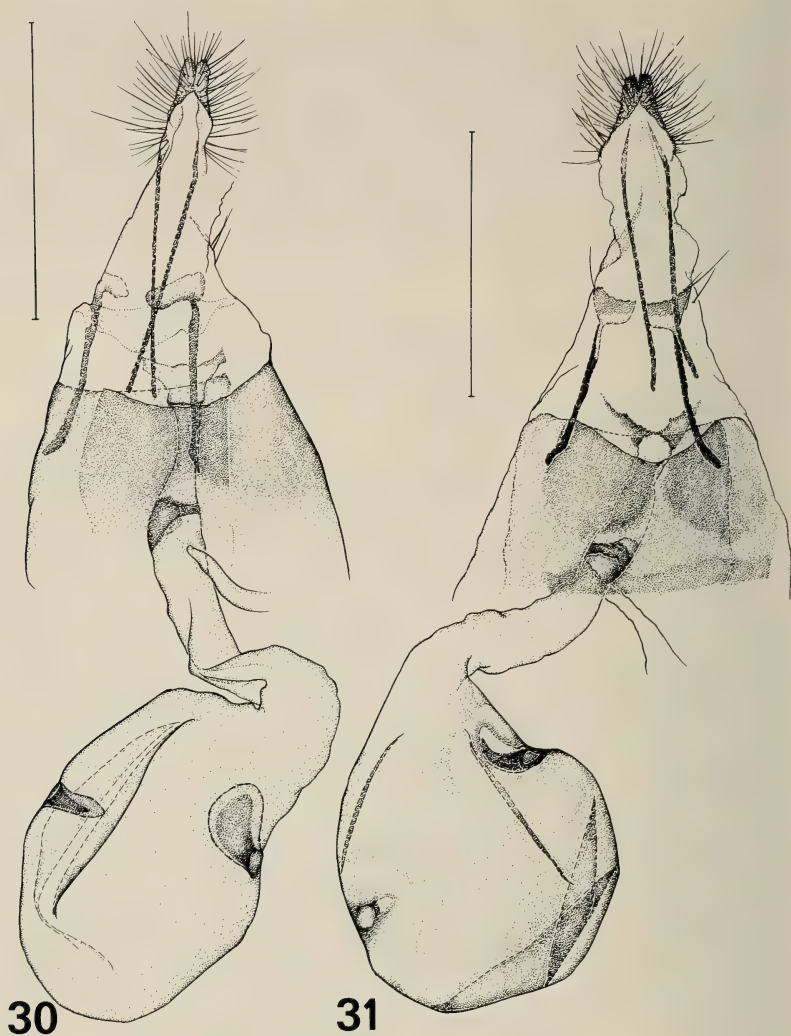
Figs. 30, 31.   Female genitalia of *Epinotia* species. **30,** *E. vertumnana,* St. Davids, Ontario, RLB slide 460 (CNC); **31,** *E. sotipena,* paratype, Putnam Co., Illinois, USNM slide 17718.

(1 ♂, genit. slide RLB 575); Warren Co., 15 Mar. 1935, Annette F. Braun (1 ♀). *Pennsylvania:* Beaver Co., New Brighton, 12 Apr. 1902, H. D. Merrick (1 ♀), 15 Apr. 1902 (2 ♀), 3 Apr. 1903 (1 ♂, genit. slide USNM 17675), 10 May 1907 (1 ♀); Dauphin Co., Rockville (1 ♂, 1 ♀, ♂ genit. slide CH 29 Oct. 1921, #2). *Ontario:* Ottawa East, 29 Apr. 1944, J. McDunnough (1 ♀, genit. slide RLB 447). *Quebec:* Chelsea, 24 Apr. 1933, G. S. Walley (1 ♀), 21 Apr. 1933, J. McDunnough (1 ♀, genit. slide RLB 450), Old Chelsea, 3 May 1939, T. N. Freeman (1 ♀). Paratypes are deposited in collections listed in the material examined for the adult, and in BMNH.

Host. Unknown.

Discussion. Male genitalia of this superficially distinctive species are similar to those of *E. laracana*. Both species have valvae that intergrade in form from gradually narrowed to somewhat abruptly narrowed, although the abruptness of narrowing is less in both than in *E. vertumnana*. Width of uncus relative to juxta is usually greater in *E. laracana* than in *E. sotipena*. The aedeagus has 14–17 cornuti in *E. laracana* and 12–14 in *E. sotipena*. Males of the two species are easily separated by length of the costal fold relative to forewing length, the fold being shorter in *E. sotipena*. Female *E. sotipena* differ from *E. laracana* in having anterior apophyses shorter relative to posterior apophyses, bursa seminalis with large spinules, and posterior signum much wider than anterior signum. Some females have debris on the papillae anales, as in *E. zandana*.

<div align="center">

Epinotia vertumnana (Zeller)
(Figs. 8, 16, 17, 22, 30)

</div>

Paediscá vertumnana Zeller (1875:310, var. d).
Epinotia zandana; Heinrich (1923:205, fig. 370); Comeau & Roelofs (1973:197); Roelofs
    & Cardé (1974:98) (not Kearfott).
Epinotia prob. *zandana*; Comeau & Roelofs (1973:194).
Epinotia atristriga Clarke (1953:228, part).
Epinotia atistriga; Comeau & Roelofs (1973:194); Roelofs & Cardé (1974:98) (misspelling
    and misidentification).
Epinotia atristriga; Roelofs & Brown, 1982:411 (not Clarke, 1953).
Epinotia sp.; MacKay (1959:64).

Adult. ♀ Type; 143 ♂, 117 ♀ examined (AMNH, ANSP, CNC, CU, INHS, MEM, MSU, RLB, UCB, USNM).
Forewing (Figs. 16, 17). FWL (nonreared): 5.5–7.0 mm; length of costal fold 0.36–0.42 FWL (22n); uniformly grayish brown or grayish brown peppered with varying numbers of white-tipped scales, some specimens with discontinuous, dark grayish brown, basal, median, and apical longitudinal streaks or with continuous longitudinal streak; rarely with dark grayish brown, subbasal and median fasciae, and preapical spot.
Male genitalia (Figs. 8, 22). Width of uncus at bifurcation 0.21–0.24 width of juxta (15n); dorsal anellar plate with straight lateral margins, apically curved outwardly; aedeagus with 6–10 cornuti (22n); valva abruptly narrowed beyond sacculus, cucullus distinctly longer than sacculus; saccular spine cluster elongate. Forty-seven preparations examined (CNC, MSU, RLB, USNM).
Female genitalia (Fig. 30). Tergum VIII as in *E. xandana*; papillae anales as in *E. laracana*; length of anterior apophyses 0.67–0.77 length of posterior apophyses (15n); posterior margin of sterigma irregularly concave; bursa seminalis without spinules; width of posterior signum 1.7–2.5 width of anterior signum (14n). Twenty-two preparations examined (AMNH, CNC, CU, RLB, USNM).
Larva. The description of *Epinotia* sp. by MacKay (1959) was based on nine larvae reared from *Crataegus* at St. David's and Merivale, Ontario. Associated adults from both localities are identified here as *E. vertumnana*.
Type. Lectotype here designated: ♀, Dallas, Tex., Boll; *vertumnana* var. d [green, handwritten label]; genitalia slide R. L. Brown 1158 [green label], Type 14336 [red label], Lectotype *Paedisca vertumnana* by R. L. Brown [red bordered label]; in MCZ. The original corroded pin holding the specimen has been clipped and the specimen has been double-mounted on a polyporus block. The specimen is in good condition, except that the right wings are rubbed. The lectotype is similar to the specimen in Fig. 16, except the median and apical streaks are continuous, and the basal streak is narrower.

Geographical distribution and flight times. Southern Ontario and Quebec (19 Mar.–20 Apr.) to E Pennsylvania (14 Mar.–15 Apr.), W to Michigan (23–31 Mar.), and S to N Mississippi (21–24 Feb.) and E Texas. Two males (UCB) tentatively identified as this species were collected during early March in Jefferson Co., Colorado.

Host. *Crataegus* (72n), reared by P. J. Chapman and S. E. Lienk in New York, and in Ontario by W. L. Putnam, T. N. Freeman, and J. McDunnough.

Discussion. Zeller described six varieties (a–f) of this species from an unknown number of specimens collected in Texas by Jacob Boll and one specimen collected by Speyer in New York. The type series in MCZ includes two specimens of "var. a", one specimen of "var. c", one specimen of "var. d", five specimens of "var. e", and two specimens of "var. f", all from Dallas, Texas. Specimens of "var. e" and "var. f" are conspecific with *E. laracana*, and "var. c" is identified tentatively as *E. xandana*. The longitudinally streaked "var. d" specimen, designated as lectotype, appears clearly conspecific with specimens reared from *Crataegus*. Specimens of "var. a" tentatively are considered synonymous with the lectotype, but these males differ in having a contrastingly paler inner margin of the forewing.

The unicolorous and fasciate forewing forms of *E. vertumnana* were misidentified by Heinrich (1923) and others as *E. zandana*. Specimens with longitudinally streaked forewings were named by Clarke (1953) as *E. atristriga*, a junior synonym of *E. zandana*. Two male specimens from Colorado have a superficially darker appearance, similar to *E. zandana*, but their genitalia cannot be differentiated from other *E. vertumnana*; collection of females from this area should clarify their identity.

In addition to smaller size and lighter color, *E. vertumnana* differs from *E. zandana* in the male genitalia by having a narrow uncus and an elongate saccular spine cluster, and, in the female, by having reduced papillae anales and long anterior and posterior apophyses. *E. vertumnana* differs from *E. laracana* and *E. sotipena* in having less than 11 cornuti and a dorsal anellar plate with straight lateral margins in the male. Females of *E. vertumnana* differ from those of *E. laracana* in having one signum much wider than the other, and from those of *E. laracana* and *E. sotipena* in having the posterior margin of the lamella postvaginalis irregularly concave rather than acutely angled.

Although the pheromone of *E. vertumnana* has not been identified, males are attracted to cis-7-dodecenyl acetate. Because this species was misidentified as "*Epinotia* sp. prob. *zandana*" and "*E. atistriga*", the attractancy of males to another form of females was considered to be an example of cross-attractancy between species (Comeau & Roelofs 1973). Fortunately, voucher specimens of both forms were retained (CU) and the correct identity now can be established.

ACKNOWLEDGMENTS

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GENERAL NOTES

MYNES GEOFFROYI GUERINI WALLACE (NYMPHALIDAE) PARASITIZED BY A TACHINID FLY

Mynes geoffroyi guerini Wallace, the white nymph, is a poorly studied nymphalid that occurs in coastal rainforests sporadically from the Claudie River in northern Queensland to near Ballina, northern New South Wales (Common & Waterhouse 1981, Australian butterflies, Angus & Robertson, 651 pp.). The larvae are gregarious and feed exclusively on the young foliage of the tall stinging trees *Dendrocnide moroides* (Wedd.) Chew and *D. photinophylla* (Kunth) Chew, and the nonstinging rainforest shrub *Pipturus argenteus* (Forster) Wedd. (Common & Waterhouse, cited above). There are four Australian species of *Dendrocnide,* while *Pipturus* is only represented by one species; both genera are from the stinging nettle family Urticaceae.

On 25 May 1985 I collected one larva of *Mynes geoffroyi guerini* from a young leaf of a mature *P. argenteus* in disturbed rainforest near Mt. Coot-tha, about 5 km W of Brisbane, Queensland. The larva, a last instar, had a fly egg behind the head. Another nine larvae were observed, but close examination showed they had not been parasitized. The parasitized larva as well as three unparasitized ones were taken to the laboratory and placed in a plastic bag with fresh leaves of the food plant. The parasitized larva pupated on 27 May. Two days later, it displayed no movement when handled (normal, healthy pupae of *M. g. guerini* usually thrash their bodies wildly about for up to 20 seconds if disturbed) and was subsequently broken to disclose an active fly maggot, which pupated 1 June 1985. Length of the fly pupa was 6.8 mm. The other butterfly larvae were reared successfully to the adult stage. The fly emerged on 6 July, after 35 days in the pupal stage. The fly was deposited in the collection of the Entomology Department, Department of Primary Industries (DPI), Indooroopilly, Queensland, and was identified by Dr. B. K. Cantrell of that Department as *Compsilura concinnata* (Meigen) (Tachinidae).

This appears to be the first published record of fly parasitism of *M. geoffroyi guerini*. *Compsilura concinnata* has been recorded as a parasite of the following Australian moths by Crosskey (1973, Bull. Brit. Mus. Nat. Hist. (Entomol.) Suppl. 21:1–221)—*Doratifera vulnerans* Lewin (Limacodidae) and *Anomis xanthindyma* Boisduval and *Brithys crini* (Fabricius) (both Noctuidae). Recently, Chadwick and Nikitin (1985, Aust. Zool. 21:587–598) recorded the Australian moth *Isotenes miserana* (Walker) (Tortricidae) and the introduced butterfly *Artogeia* (*Pieris*) *rapae* (L.) (Pieridae) as pupal hosts of *C. concinnata*.

The parasitoid fly *C. concinnata* has a widespread distribution, and is known from the Palearctic region (including Japan), Africa, the Oriental Region to Australia, and has been introduced into North America (Arnaud 1969, Pan-Pacific Entomol. 45:77; 1978, USDA Misc. Pub. No. 1319:149–168). The species is one of the most widely reared parasites of Lepidoptera in Europe (Herting 1960, Mono. Ang. Entomol. Nr. 16:55–57) and North America (Arnaud, cited above). These authors each record over 100 species of lepidopteran hosts from a wide range of families and genera of butterflies and moths, indicating that *C. concinnata* is a generalist and opportunistic fly in larval feeding habits and the type of habitat frequented. Although Australian host records are scanty, they do show similar trends of nonspecificity to any one group of Lepidoptera.

The pupal duration of 35 days of *C. concinnata* recorded here is considerably longer than the 11–14 days recorded for another tachinid fly parasite of Australian butterflies, *Winthemia neowinthemioides* (Townsend) (Smithers 1973, Aust. Entomol. Mag. 1:37–40; Hawkeswood 1986, in review). Whether this longer pupation period results from species-specific differences or is due to the colder conditions under which *C. concinnata* was reared (during winter) awaits further research.

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AN OVIPOSITION "MISTAKE" BY *BATTUS PHILENOR* L. (PAPILIONIDAE)

Although oviposition on plants unsuitable for larval development occurs among the Lepidoptera (Berenbaum 1981, J. Lepid. Soc. 35:75 and references therein), the actual egg-laying episodes have rarely been witnessed. I report here direct field observation of an oviposition "mistake" by the pipevine swallowtail, *Battus philenor*. This record is particularly noteworthy because the errant female was one for which a detailed field record of egg-laying activity over three weeks was accumulated.

On 7 April 1981, at a field site in Kirby State Forest, Tyler Co., Texas, Mark D. Rausher and I observed a *Battus* female deposit a single egg on a leaf of *Smilax laurifolia* L. (Liliaceae). This event represents the only oviposition by this butterfly species on a plant outside the genus *Aristolochia* (Aristolochiaceae) noted in more than eight years of fieldwork on the Texas population by me and colleagues. Our studies included observations of hundreds of ovipositing butterflies and tens of thousands of landings on nonhost foliage. No *Aristolochia* plants were present within 2 m and the female had not discovered any host plants in the previous 2 min of observation. Although I intended to follow the progress of larval development on the plant, both egg and leaf were gone on the third day after oviposition. Nevertheless, 25 larvae freshly hatched from eggs laid by captive females on the native E Texas host plants, *A. reticulata* Nutt. and *A. serpentaria* L., and placed on cuttings of young *Smilax* foliage failed to consume any leaf material and did not survive to the second instar. By contrast, another 25 larvae fed on cuttings of both *Aristolochia* hosts progressed normally through the first instar and many eventually pupated.

Most remarkable about the egg deposition on *Smilax* was the insect's extended period of investigation; several minutes of fluttering over the leaf and circling about the plant preceded the aberrant oviposition. During oviposition, *Battus* females alight frequently on nonhost plants upon which they drum their foretarsi, presumably tasting the leaf surface with tarsal chemoreceptors (Feeny, Rosenberry & Carter 1983, pp. 27–76 *in* Herbivorous insects: Host-seeking behavior and mechanisms, Academic Press, New York, and references therein). Most individuals leave nonhost plants immediately after landing and resume searching for host plants.

The extensive history of searching by this particular *Battus* female suggests several explanations for the anomalous egg deposition. First, the female may have been more prone to oviposit on an unsuitable plant due to low rates of discovery of the principal *Aristolochia* hosts. The rate of discovery of *Aristolochia* plants in the minutes before the *Smilax* oviposition was indeed low (0.19 host plants/min vs. a mean of 1.02 host plants/min for 6 other observation periods). Since no eggs were laid on several hosts discovered just minutes earlier, however, the female was not evidently "desperate" to lay eggs.

Alternatively, the female may have suffered some deterioration of the sensory apparatus required to identify a host plant after landing. Extremely worn and tattered at the time she oviposited on *Smilax*, the female had been first marked two weeks previously. Only 1 other butterfly of almost 200 marked was followed as long. The efficiency with which the aging female landed on host plants did indeed decline in successive recaptures (Fig. 1). Since relative host density did not change significantly over this period, the female was apparently identifying host plants before landing less accurately as she aged. Possibly, she was discriminating between hosts and nonhosts less accurately after landing as well.

Finally, the mistaken deposition may have resulted from the female's previous experience with host plants. Pipevine swallowtail butterflies learn to search for the leaf shape of preferred host plants (Papaj 1986, Anim. Behav. 34:1281–1288). This particular female, for example, almost always alighted on broad nonhost leaves resembling the broad-leaved *A. reticulata* (Fig. 1). The *Smilax* plant on which an egg was laid consisted of a solitary, newly formed broad leaf on a short stem, and bore a striking visual resemblance
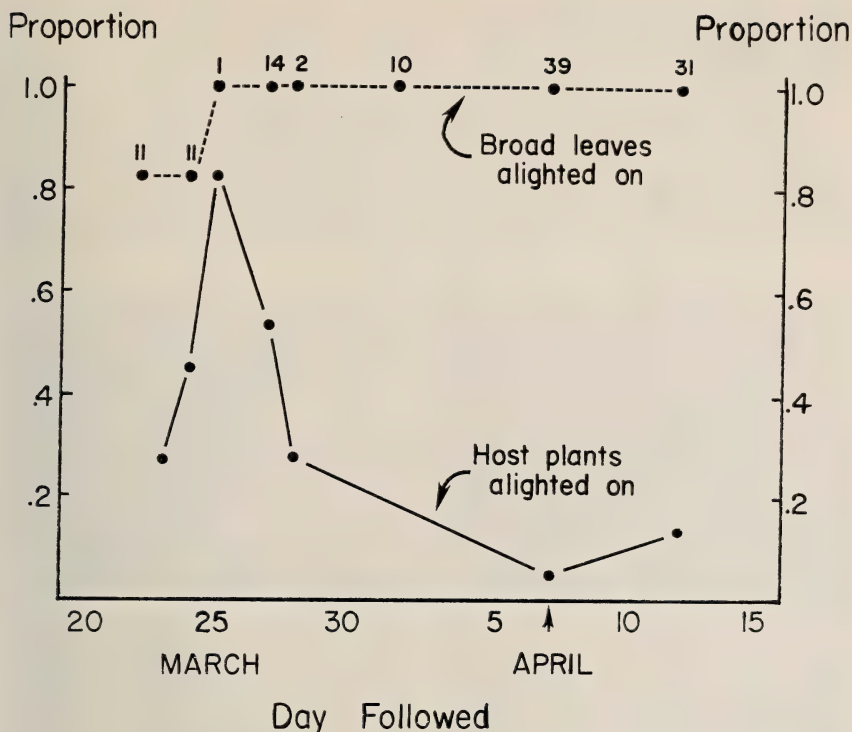
FIG. 1. Record of host-landing efficiency and leaf-shape response over time. Solid line indicates time course of host-landing efficiency, expressed as proportion of all plants alighted on that were *Aristolochia*. Dotted line indicates time course of leaf-shape preference, expressed as fraction of all nonhost leaves alighted on that were broad. Number above each point indicates sample size on each observation day. Arrow indicates day of anomalous egg deposition.

in color, leaf shape, and growth form to phenologically young *A. reticulata* plants which are highly preferred for oviposition (Rausher 1980, Evolution 34:342–355; Papaj & Rausher 1987, Ecology, in press). Possibly, the experienced female became so positively responsive to the visual stimuli of young *A. reticulata* foliage (which the young *Smilax* leaf mimicked well enough to deceive two human observers) that conflicting negative responses to nonhost chemotactile cues were eventually suppressed.

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EMERGENCE OF *TISCHERIA IMMACULATA* (BRAUN) (TISCHERIIDAE)
FROM LEAVES OF *CEANOTHUS GRISEUS* L.

Tischeria immaculata (Braun) larvae mine leaves of *Ceanothus griseus* L., a native
ornamental in Washington State and California (Braun 1915, Entomol. News 26:271–
273; Fasoranti 1983, Z. Angew. Entomol. 96:270–476). Biology and mining habits were
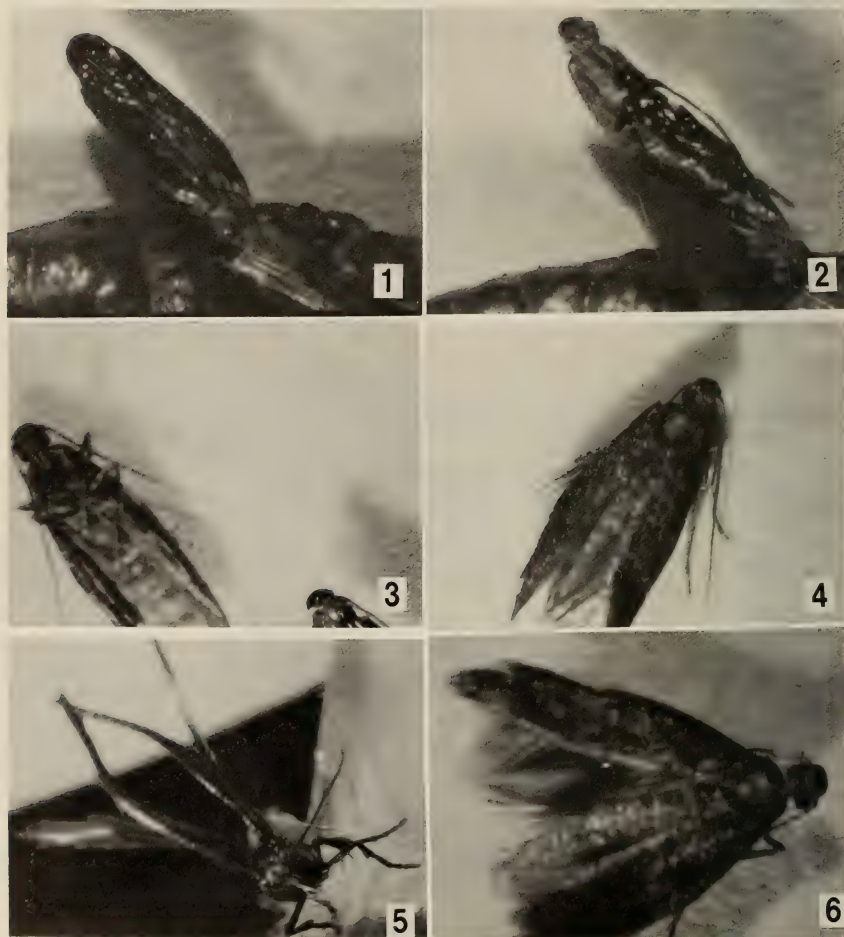
FIGS. 1–6.   Emergence of *Tischeria immaculata*. **1, 2,** Insect thrusts itself from the
mine and withdraws legs; **3,** Insect falls on back and rests for a few seconds; **4,** It flips
over suddenly and stays in this position for about 15 seconds; **5,** Wing pumping, expan-
sion, and drying accompanied by circular movements for 45 seconds; **6,** Wing beating
before insect rests.

elucidated in Washington by Fasoranti (1984, Can. Entomol. 116:1441–1448). Adults appear at the beginning of May, and there is a short cycle of development during the warm weather between May and August. The next generation takes longer, from August through May of the following year. Mating and egg laying starts immediately after emergence.

Emergence takes place mostly in the evening (1750–2400 h). Time of emergence provides some protection against the insect's principal predator, the dark eyed junco, *Junco hyemalis* L. Emergence also is temperature dependent. In field and laboratory, emergence occurred only at temperatures between 20–22°C. Insects rarely emerged below or above these temperature limits. A typical exit hole is crescentic, about 0.15–0.20 mm long (N = 350), with the convex side toward the end of the mine. The center of the crescent is about 0.20 mm from the end of the mine.

Under controlled conditions (21°C and 70% RH), emergence of 75 adults was timed and photographically documented with a 35 mm camera attached to a microscope using Panatomic X film. The subjects were illuminated with light from two opposing sources. A typical sequence of emergence is shown in Figs. 1 to 6. The whole process takes between 6–7 minutes.

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UNUSUAL PREDATOR DAMAGE TO *CARTEROCEPHALUS SILVICOLUS* (MEIGEN) (HESPERIIDAE)

Bird-inflicted wing damage in Lepidoptera that fold their wings above their bodies at rest was classified into two categories by Beck and Garnett (1983, J. Lepid. Soc. 37:289–300). To continue the earlier classification proposed by Sargent (1976, Legion of night, Univ. Mass. Press, Amherst, Massachusetts, 222 pp.), who worked with noctuid species, the new categories were called Type IV (for bilaterally symmetrical tears roughly parallel to the main wing veins) and Type V (for beak imprints which cross the main wing veins

FIG. 1.   *Carterocephalus silvicolus* (Meigen) ♂ (dorsal), showing Type Vb wing damage.

FIG. 2.   Position of specimen when held by bird, reconstructed from cut-out tracings of the four wings.

at roughly right angles). A subcategory of Type V (Type Vb) was proposed to accommodate beak imprints across all four wings. We assumed this situation would always result in a successful capture, and Type Vb was included only for completeness.

Since then, a specimen showing "hypothetical" Type Vb damage came to our attention (Fig. 1). Unfortunately, nothing is known about the circumstances surrounding its capture other than the data on the specimen label: Akademici Raros, Novaibirsok, USSR; 20-vi-1978; coll; V. Dubatolov. Despite this, two facts are clear. First, the insect was grasped by a bird's beak firmly enough to leave distinct areas devoid of scales on all four wings. Second, the insect was subsequently released. We believe release was not caused by the insect's efforts to escape, since no significant tears or other signs of pulling free are discernible. It is also unlikely that the insect startled the bird since all wings were immobilized and, from the position of the beak imprints, the legs and antennae were directed away from the bird's face (Fig. 2 or its mirror image).

Hypotheses explaining the skipper's release include 1) an error in prey manipulation by the bird, 2) the possibility of some allomonal product of the skipper, and 3) an extrinsic startle from outside the predator-prey system. The first is possible and the second unlikely, since we know of no references to vertebrate-effective allomonal products produced by members of this genus. We prefer the third possibility. If the bird was not processing prey at the site of capture but bringing it instead to nestlings, there would be time during which the bird could have been startled into releasing its prey by some extrinsic factor.

We thank Bálint Zsolt of Budapest, Hungary, for the *C. silvicolus* specimen, currently in the collection of the senior author, and ultimately to be deposited in the Florida State Collection of Arthropods, Gainesville, Florida, USA.

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FOUR NEW UNITED STATES RECORDS OF MOTHS FROM TEXAS

The four moths illustrated here represent new records for the United States and were collected in extreme S Texas in UV light traps. The lower Rio Grande valley has been drastically modified by the environmental changes that accompany rapid population growth, intensive agricultural land use, and widespread aerial spraying of pesticides. Few natural areas remain, and the consequences of this are becoming apparent. One endemic moth, *Agapema solita* Ferguson (Saturniidae), formerly common around Brownsville and known only from southern Texas (Ferguson *in* Dominick et al. 1972, Moths of America north of Mexico, fasc. 20.2B, E. W. Classey Ltd., London), has not been seen since 1956, and may now be extinct, or nearly so, as a result of habitat destruction. Probably there are other not as well documented examples.

In spite of the loss of habitat, unusual species of Lepidoptera continue to appear, including many new records for the United States (Kendall & McGuire 1984, Bull. Allyn Mus. Entomol. 86:1–50; Blanchard & Knudson 1985, J. Lepid. Soc. 39:1–8). Some are probably individual nonbreeding immigrants from a large reservoir of species that still exists in the Sierra Madre Oriental of northeastern Mexico, where rich tropical to montane temperate zone forests are found within 322 km of the border. However, some Mexican species do become established periodically in S Texas, later to be extirpated by low temperatures or drought. One case of temporary occurrence was reported but subsequently overlooked, and is perhaps worth citing here. Adults of the pantropical bean pod borer, *Maruca testulalis* (Geyer) (Pyralidae, Pyraustinae), were reared from larvae feeding on string beans at Olmito, Cameron Co., Texas (Williamson 1943, J. Econ. Entomol. 36:936–937). This species has not again been reported from the continental United States, although it can thrive in agricultural environments in warmer climates (Ferguson 1983, Pests not known to occur in the United States or of limited distribution, No. 40, PPQ, Animal & Plant Health Inspection Service, USDA). Details of the new records follow.

Euprosterna lacipea Druce (Limacodidae), Brownsville, Cameron Co.,7 August 1976, 1 male; Santa Ana Nat'l. Wildlife Refuge, Hidalgo Co., 28 May 1982, 8 males (Fig. 1); 14 May 1983, 1 male; 4 August 1986, 3 males; collected by E. C. Knudson. Body and wings dark brown, lightly frosted with light gray; bands on forewing upper side light gray; length of forewing 9–10 mm. This species appears well established in S Texas, though apparently was not present before 1976. There are three Mexican specimens in the U.S. National Museum (USNM) from Vera Cruz and Colima.

Molybdogompha polymygmata Dyar (Geometridae), Santa Ana Nat'l. Wildlife Refuge, Hidalgo Co., 23 September 1980, 1 female (Fig. 2), collected by Knudson. Wing upper sides light yellowish brown with multiple, transverse parallel, blackish striations and a regular subterminal row of ocellate spots; terminal line of silvery, interrupted dashes; length of forewing 8.5 mm. The type specimen and a second specimen are in the USNM and both are from Vera Cruz. A third Mexican specimen was collected by Knudson near Cd. Valles, San Luis Potosí, 28 November 1978, and is in the American Museum of Natural History. The relations of this genus within the Geometridae are unclear, but its superficial appearance indicates that it might belong to the tribe Baptini (Ennominae).

Eubaphe medea (Druce) (Geometridae), Bentsen State Park, Hidalgo Co., 27 May 1982, 3 males (Fig. 3), collected by Knudson. Body orange; wings translucent pale orange with opaque bright orange discal patch; middle of forewing costal margin with fold; length of forewing 14–15 mm. This species has apparently been collected in Mexico, but the locality and present specimen location are not known to us. It is otherwise known from Guatemala, Honduras, Costa Rica, and Panama (Fletcher 1954, Zoologica [New York Zool. Soc.] 39:153–166).

Psamathia placidaria (Walker) (Epiplemidae), Santa Ana Nat'l. Wildlife Refuge, 30
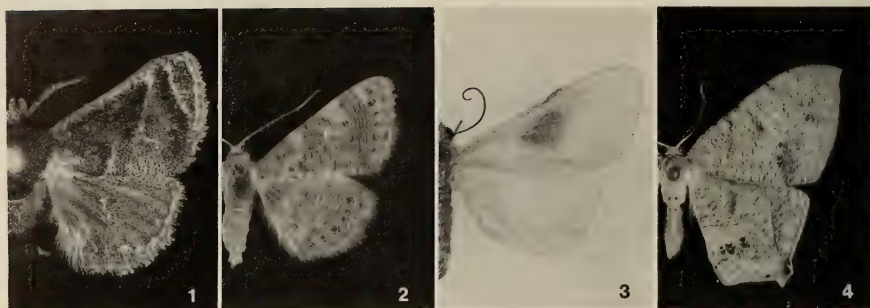
FIGS. 1–4. **1,** *Euprosterna lacipea* Druce; **2,** *Molybdogompha polymygmata* Dyar;
3, *Eubaphe medea* (Druce); **4,** *Psamathia placidaria* (Walker).

November 1981, 1 male (Fig. 4), collected by Knudson. Body and wings grayish brown
above and below; wings above with innumerable, broken, blackish striations and black
dots over lower median area of forewing and near anal margin of hindwing; hindwing
produced as a short, black-marked, obliquely truncated tail; length of forewing 18 mm.
This species ranges from Mexico to Venezuela. In Mexico, it has been collected in Ta-
maulipas by Knudson and Alma Solis.

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NEW HOST RECORDS FOR *EUPLOEA CORE CORINNA* (MACLEAY) (NYMPHALIDAE)

During the course of taxonomic studies on Asclepiadaceae and Apocynaceae, numerous
observations of oviposition, feeding and pupation of the crow butterfly, *Euploea core
corinna* (Macleay) were made. This butterfly is widely distributed in northern and east-
ern Australia (Common & Waterhouse 1981, Butterflies of Australia, Angus & Robertson,
Sydney) with temperature requirements and suitable host plants restricting the subspecies
range (Scheermeyer 1985, Aust. J. Zool. 33:339–348). In a review of host plant records
for this Australian species, various species of Asclepiadaceae and Apocynaceae, either
naturalized or cultivated, were listed, as well as native species of these families and the
Moraceae (Scheermeyer & Zalucki 1985, Aust. Entomol. Mag. 11:87–90). Some host
plants have been demonstrated to significantly affect development times, weights, size,
and mortalities at all stages of the life cycle (Rahman, Zalucki & Scheermeyer 1985, J.
Aust. Entomol. Soc. 24:95–98).

Euploea core corinna is known at times to oviposit on unsuitable hosts (Kitching &
Zalucki 1983, Aust. Entomol. Mag. 10:64–66) and I have observed eggs on *Mammillaria
gracilis* Pfeiff. (Cactaceae), but no larval feeding. In some instances, limited larval feed-
ing may occur as observed on the Madagascan *Cynanchum compactum* Choux and three

unidentified *Cynanchum* species related to *C. mahafalense* Jum. & Perr. (Asclepiadaceae).

I observed completion of the life cycle of the butterfly to the adult stage (new records indicated *) on the following hosts in cultivation at the localities and dates listed.

1. In April 1986, on the African *Adenium obesum* Balf.* and *A. multiflorum* Kl.* (Apocynaceae) at the Mt. Coot-tha Botanic Gardens, Brisbane, Queensland (27°29′S, 153°00′E). Both young and mature leaves were eaten. No feeding was observed on adjacent plants of the related Madagascan *Pachypodium lamieri* Drake.

2. During summer 1985–86 at Didcot, Queensland (25°28′S, 151°52′E), on the Australian *Sarcostemma australe* R. Br. subsp. *australe*, *S. australe* tentative subsp. nov. 1 and *S. australe* tentative subsp. nov. 2 (Forster, unpubl.), but not on adjacent plants of the African *S. viminale* (L.) R. Br., *S. vanlessenii* Lavr., *S. stolonifera* Adams & Holland and *S. socotranum* Lavr. (Asclepiadaceae). Only young shoots were eaten.

3. During summer 1985–86 at Annerley (27°31′S, 153°03′E) and Strathpine (27°24′S, 152°57′E), Brisbane and Didcot, on young shoots and leaves of the Australian *Hoya australis* R. Br. ex Traill., *H. sana* F. M. Bail.* and *H. macgillivrayi* F. M. Bail.*, the New Guinean *H. archboldiana* C. Norman* and Asian *H. carnosa* (L.) R. Br.*, but not on adjacent plants of the Australian *H. nicholsoniae* F. Muell., *H. poolei* C. T. White & Francis and various unidentified species of Section *Eriostemma* (Asclepiadaceae).

4. During late summer 1986 at Didcot on old leaves and shoots of *Brachystelma microstemma* Schltr.* (syn. *Microstemma tuberosum* R. Br., Forster 1985, Taxon 34: 318–319) (Asclepiadaceae).

All of these host plants (except *Brachystelma*) possess obvious white latex, which is probably ingested by the *Euploea* larva. Australian *Hoya australis* and certain populations of *Sarcostemma australe* s.l. have been found to be highly toxic on ingestion by domestic livestock, with as yet unsatisfactorily determined chemical components of the latex implicated (Everist 1981, Poisonous plants of Australia, Angus & Robertson, Sydney). Presumably the *Euploea* larvae are not affected by this toxic principle.

The chemical composition of latex and leaf surface waxes of different species of *Hoya* differs in the proportions and presence of various triterpenols and their esters (Baas & Niemann 1979, Planta Medica 35:348–353; Baas, Warnaar & Niemann 1981, Acta. Bot. Neerl. 30:257–263; Warnaar 1984, Phytochemistry 23:1049–1053). As the composition of these components appears to be species specific, it would be of interest to investigate whether or not selective *Euploea* feeding on different species of *Hoya* is correlated with these chemical differences in the host plants.

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BOOK REVIEW

THE BUTTERFLIES OF NORTH AMERICA: A Natural History and Field Guide, by James A. Scott. 1986. Stanford University Press, Stanford. 583 pp., 64 color plates. $49.50.

To generations of American collectors, Holland's *Butterfly Book* was *the* butterfly book. For eastern North America, it was superseded in 1951 by Klots' *Field Guide*. No equivalent work appeared in the West until 1986, when Tilden & Smith's *Field Guide* in the Peterson series finally came out. The uneven and flawed Howe *Butterflies of North America* (1975) was supposed to be an update of Holland, but never really "caught on." Meanwhile, there had been a proliferation of regional treatments, from Shapiro's *Butterflies of the Delaware Valley* (1966) and Pyle's *Watching Washington Butterflies* (1974) through Emmel & Emmel on southern California, Dornfeld on Oregon, Ferris and Brown on the Rockies, and most recently Opler & Krizek on the eastern fauna again. Scott's new book, ambitiously also titled *The Butterflies of North America*, is another attempt to encompass the whole fauna as Holland had done. The result is a visually striking book, and one that belongs in every lepidopterist's library. But it is not without its problems.

While regional treatments were proliferating, taxonomic problems were, too. A great deal of ink, and many hurt feelings, have been spent in wrangling over the "correct" names of North American butterflies. The controversy is too recent as history to require recapitulation here, but in a nutshell, most of the names familiar for two or three generations were altered by a combination of generic splitting and, later, a zealous attempt to make all specific epithets agree in gender with their current genera. The latter represented a strict interpretation of the Code. The former was voluntary, and represented an interpretation of the concept of the genus which was in tune with what prominent amateurs in Europe were doing but, in the opinion of many, was inadequately justified in biology. There are no external standards of right or wrong here; the concept of the genus is thoroughly nebulous and must forever be. Meanwhile, collectors need to put names on their beasties. Anyone who tries to use Scott and almost any other recent book *together,* and who is not already taxonomically sophisticated, may decide to give up butterflies altogether and take up Latin blank verse instead.

The reason for this is that Scott is diametrically opposed to the trend of the times. He is a "lumper." He lumps at both generic and specific levels; thus one finds most of the familiar generic names restored (which I applaud)—but sometimes it becomes rather difficult to figure out what *species* is meant. His judgment is very likely to be correct (as, for example, on putting *ferrisi* as a subspecies of *Lycaena rubidus*, and ignoring the mysterious Johnson *Mitouras* altogether) in a majority of cases, but the justification for it is often unstated. In other cases (putting *all* of the Cupressaceae-feeding *Mitoura* in North America except *hesseli* in one huge species, *gryneus*, for example) the lumping is so ambitious that it is very likely wrong—and certain to inspire much indignation.

As a specimen problem case, consider the *Hesperia* "comma complex." I am not convinced that the Nearctic taxa should be put as subspecies of the Palearctic *comma* at all (ditto the *Coenonympha* "tullia complex"), but be that as it may, there is a generally accepted set of subspecies in western North America, described, defined, and mapped in some detail in MacNeill's monograph, and not substantially altered in any taxonomic work appearing since except for being put under *comma*, instead of *harpalus* as a specific epithet. We happen to be working very hard on the genetics of the northern California members of this complex, so I turned to Scott's treatment—and was flabbergasted. Instead of the ten subspecies in Tilden and Smith, Scott recognizes eight, plus a new unnamed one. One of the eight is his own, and does not appear in Tilden and Smith (*oroplata*). The treatment of the California populations is revolutionary: Scott puts ssp. *manitoba* "south in the Cascades to northern California," while Tilden and Smith, following MacNeill, have it south only to northern Washington and Wyoming. Ssp. *oregonia* disappears into *manitoba* without a word. Ssp. *yosemite* is given by Scott as ranging over "west slope of the Sierra Nevada, southern California, and the Inner Coast Range"—

thus silently incorporating both *tildeni* and *leussleri*. The figured specimen shows a phenotype never remotely approached on the Sierran west slope, whence comes the type. That is not surprising; it is from the Bay Area (Santa Clara County)! And so on.

And one could go on, easily, for many pages. But the message can be defined succintly: Scott may be right a lot of the time, but a popular book—a "field guide and natural history"—is not the appropriate place to shake up formal taxonomy like this. There is no one to enforce taxonomic decisions except journal editors, and they are not of any one mind. *What is the collector to do?*

All this said, I must admit that Scott's book is beautiful. The color plates are all photographic, and are by far the most useful ever produced in this country for identification purposes, even if one is completely confused about the names. This is particularly true of the skippers, most of which have never been reproduced as color photographs before. The specimens in the plates are identified by the number of the species in the text. This makes it easy to reference from plate to text. To go the other way is to hunt and peck, because the specimens are not arranged in numerical order.

The host plant information is copious, not referenced, and apparently subject to some winnowing (and occasional critical comment), but inadequately qualified as to local specialization vs. species-wide breadth. The range maps include much recent information, and they correct a few errors that appeared in the Opler & Krizek book. The text is full of biological information, mostly attributed, which is unfamiliar and much of which has certainly never been published before. There is a splendid and entirely novel section on larval morphology, complete with setal maps and a brand-new key to first-instars. There is a "hostplant catalogue" at the back which enables the reader unarmed with the two volumes of Tietz to go from the identity of a plant to possible identities of the larva found eating it (but of course, this presupposes that it is a *butterfly*, not a moth, larva).

In short, an amazing, impressive, infuriating book that will give us all much to argue about for decades. I am reminded of the lovers in a Noel Coward play who cannot live with *or* without each other. As I continue to mine this book for goodies and to fume over this or that piece of lumping or offhand undocumented zinger, I am thankful that I no longer maintain a private collection and that the responsibility for curating our institutional one is not mine.

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(New names in **boldface**)

NOTICE TO CONTRIBUTORS

Contributions to the *Journal* may deal with any aspect of the collection and study of Lepidoptera. Short manuscripts concerning new state records, current events, and notices should be sent to the *News*, June Preston, Editor, 832 Sunset Drive, Lawrence, KS 66044 U.S.A. *Journal* contributors should prepare manuscripts according to the following instructions.

Abstract: An informative abstract should precede the text of all articles.

Text: Manuscripts should be submitted in *triplicate*, and must be typewritten, *entirely double-spaced*, employing wide margins, on one side only of white, 8½ × 11 inch paper. Titles should be explicit and descriptive of the article's content, including the family name of the subject, but must be kept as short as possible. The first mention of a plant or animal in the text should include the *full scientific name* with *author*. Measurements should be given in *metric units*; times should be given in terms of the *24-hour clock* (0930 h, not 9:30 AM). Underline only where *italics* are intended. References to footnotes should be numbered consecutively, and the footnotes typed on a separate sheet.

Literature Cited: References in the text of articles should be given as Sheppard (1959) or (Sheppard 1959, 1961a, 1961b) and all must be listed alphabetically under the heading LITERATURE CITED, in the following format:

SHEPPARD, P. M.   1959.   Natural selection and heredity. 2nd. ed. Hutchinson, London. 209 pp.
———   1961a.   Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10:165–216.

In general notes, references should be given in the text as Sheppard (1961, Adv. Genet. 10:165–216) or (Sheppard 1961, Sym. R. Entomol. Soc. London 1:23–30).

Illustrations: Only half of symmetrical objects such as adults with wings spread should be illustrated, unless whole illustration is crucial. Photographs and drawings should be mounted on stiff, *white* backing, arranged in the desired format, allowing (with particular regard to lettering) for reduction to their final width (usually 4½ inches). Illustrations larger than 8½ × 11 inches are not acceptable and should be reduced photographically to that size or smaller. The author's name, figure numbers as cited in the text, and an indication of the article's title should be printed *on the back* of each mounted plate. Figures, both line drawings and halftones (photographs), should be numbered consecutively in Arabic numerals. The term "plate" should not be employed. Figure legends must be typewritten, double-spaced, *on a separate sheet* (not attached to the illustrations), headed EXPLANATION OF FIGURES, with a separate paragraph devoted to each page of illustrations.

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of the

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Cover illustration: Semilooping larva of the strange noctuid *Phyprosopus callitrichoides* on *Smilax.* Sketch by Mark Klingler, Carnegie Museum of Natural History. Suggested by John E. Rawlins.

Journal of
The Lepidopterists' Society

STATUS AND HABITATS OF POTENTIALLY ENDANGERED LEPIDOPTERA IN OHIO

John A. Shuey, Eric H. Metzler, David C. Iftner,
John V. Calhoun, John W. Peacock, Reed A. Watkins,
Jeffrey D. Hooper and William F. Babcock

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ABSTRACT. The status of eight species that are potential candidates for addition to the U.S. list of endangered species was assessed in 1985. Two of these, *Phyciodes batesii* (Nymphalidae) and *Acronicta albarufa* (Noctuidae), are known only from literature records, and their occurrence in Ohio is unverified. Three species, *Neonympha mitchellii* (Satyridae), *Catocala marmorata* (Noctuidae), and *Catocala pretiosa* (Noctuidae), have not been collected in Ohio for more than 30 years. Three species are extant in Ohio: *Lycaeides melissa samuelis* (Lycaenidae), *Speyeria idalia* (Nymphalidae), and *Erythoecia hebardi* (Noctuidae). Further investigations into the ecological requirements of all the species are suggested, as well as habitat manipulations and acquisitions to insure their continued survival in Ohio. Special emphasis should be placed upon *melissa* and *hebardi* because both are limited to small geographic areas in the State. *Speyeria idalia* seems secure in unglaciated Ohio but has undergone a decline in glaciated areas. Conservation efforts for this species should be concentrated on the isolated populations in glaciated Ohio.

Additional key words: surveys, conservation.

Eight species of Ohio Lepidoptera, four butterflies and four moths, have been identified as being potentially threatened or endangered (Anonymous 1984). The species are: 1) *Lycaeides melissa samuelis* Nabokov (Lycaenidae), 2) *Speyeria idalia* (Drury) (Nymphalidae), 3) *Phyciodes batesii* (Reakirt) (Nymphalidae), 4) *Neonympha mitchellii* French (Satyridae), 5) *Acronicta albarufa* (Grote) (Noctuidae), 6) *Catocala marmorata* W. H. Edwards (Noctuidae), 7) *Catocala pretiosa* Lintner (Noctuidae), and 8) *Erythoecia hebardi* Skinner (Noctuidae).

Concerning the butterflies, *P. batesii* is known only from literature records, and its occurrence in Ohio is unverified. *Neonympha mitchellii* has not been collected in Ohio for more than 30 years. These species

may occur in Ohio, but unless they are rediscovered, no action can be directed toward their preservation. *Lycaeides melissa samuelis* and *S. idalia* are extant in Ohio, and further investigation into their ecological requirements is necessary to insure their continued survival in the State.

Of the four species of moths, only one, *E. hebardi*, has recently been collected in Ohio. One, *A. albarufa*, is known only from literature records, and the other two, *C. marmorata* and *C. pretiosa*, have not been seen in Ohio since the end of the nineteenth century. Based on the written reports and the numbers of extant specimens, it can be deduced that *C. pretiosa* was not rare, whereas *C. marmorata* was.

The brevity of some of the species reports to follow here is evidence of how little is known about them. This is perhaps due to their rarity, but dearth of written information is typical of economically unimportant Lepidoptera. Although many collectors have "local" knowledge, it is rarely written down. Specimens in collections provide some clues, but researchers frequently work without much information.

Information on species potentially threatened and endangered in Ohio has not been adequately compiled. Many areas in Ohio provide habitats for potentially threatened or endangered species of Lepidoptera. Data on these species and their habitats are needed to enhance our ability to make biologically sound policy and management decisions concerning the species and their habitats.

The Ohio Lepidopterists, an organization dedicated to advancing the scientific knowledge of Lepidoptera, conducted a one-year study of the habitats and plant associations of the target Lepidoptera species, their presence or absence in selected habitats, and their historical occurrence in Ohio. The following is a summary of findings.

SPECIES ACCOUNTS

Lycaeides melissa samuelis

Historical distribution. The eastern subspecies *samuelis* occurs in scattered colonies in the Great Lakes area and the Northeast (Opler & Krizek 1984). This insect, the Karner blue, has long been known from Ohio (Rawson & Thomas 1939, Nabokov 1949, Forbes 1960, Price 1970, Opler & Krizek 1984). In recent years, it has been recorded only from an area adjacent to the Schwamberger Preserve in Lucas Co. (Fig. 1). A single record from Summit Co. (Albrecht 1982) was based on a misidentification.

Habitat and plant associations. *Lycaeides melissa samuelis* inhabits sandy pine barrens, oak openings, lakeshore dunes and sandy pine prairies. These habitats must support the lupine, *Lupinus perennis* L., the only known larval hostplant of *samuelis*. *Lupinus perennis*, itself considered "potentially threatened" in Ohio (Cooperrider 1982), requires periodic fire or other disturbances to compete with woody plants (Dirig & Cryan 1976, Miller 1979). Lupine grows in sandy soils, and is important in stabilizing open sand. However, as the soil is stabilized, trees become established, and herein lies the problem for the continued survival of the Karner blue. Apparently, the butterfly will not utilize shaded lupine plants. Originally, natural wildfire was probably an important factor in
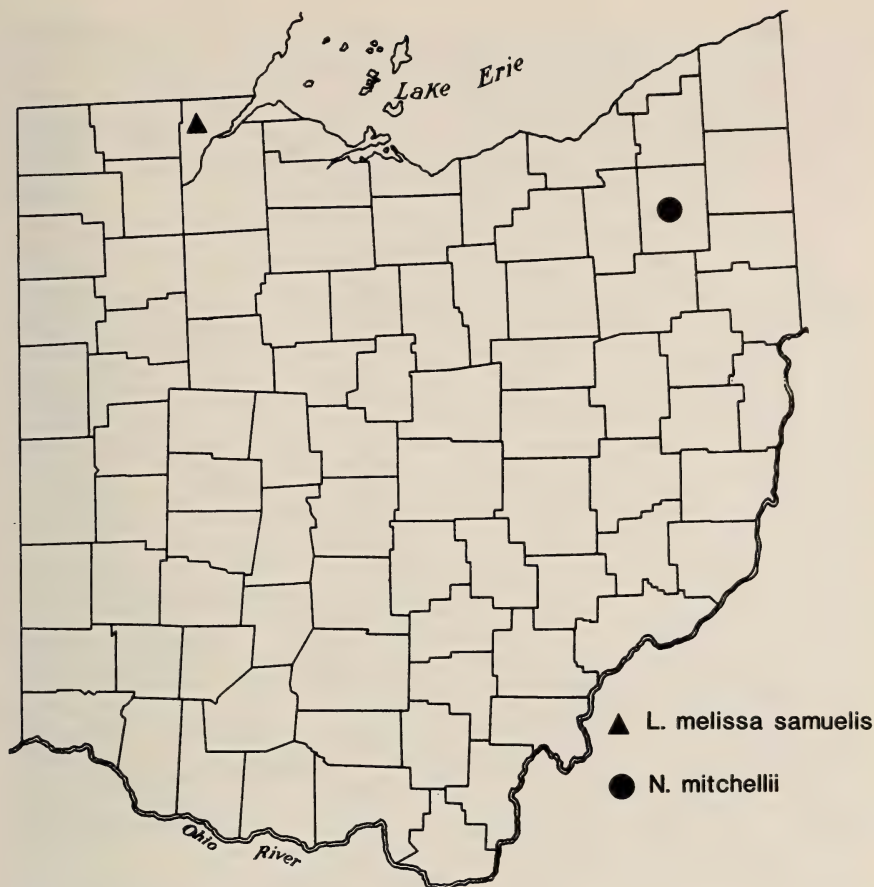
FIG. 1. Distribution of *Lycaeides melissa samuelis* and *Neonympha mitchellii* in Ohio, based on examined specimens.

controlling trees that encroached the prairies and other openings. The recent advent of fire prevention has resulted in many of the prairies of the area becoming overgrown with shrubs. Some of these areas have become quickly forested. One of the many results of this has been the near extinction of the Karner blue in Ohio. The last known population could easily become extinct despite efforts to protect it.

Current distribution in Ohio. Presently, a small area in and near the Schwamberger Preserve harbors the only known natural population of the Karner blue remaining in Ohio. Several other potential habitats in Lucas Co. have been surveyed by the Ohio Lepidopterists and others in recent years. Only one other population of *samuelis* was discovered, an introduced small colony in Oak Openings Metropark near Toledo. Scattered populations of lupine were discovered at a few sites in Lucas Co. (Campbell State Nature Preserve, and Oak Openings Metropark system) and in Henry Co., but no *samuelis* were seen at any of these locations.

Discussion. Presently, the outlook for the Karner blue in Ohio is not favorable. The butterfly has been virtually eliminated from the Oak
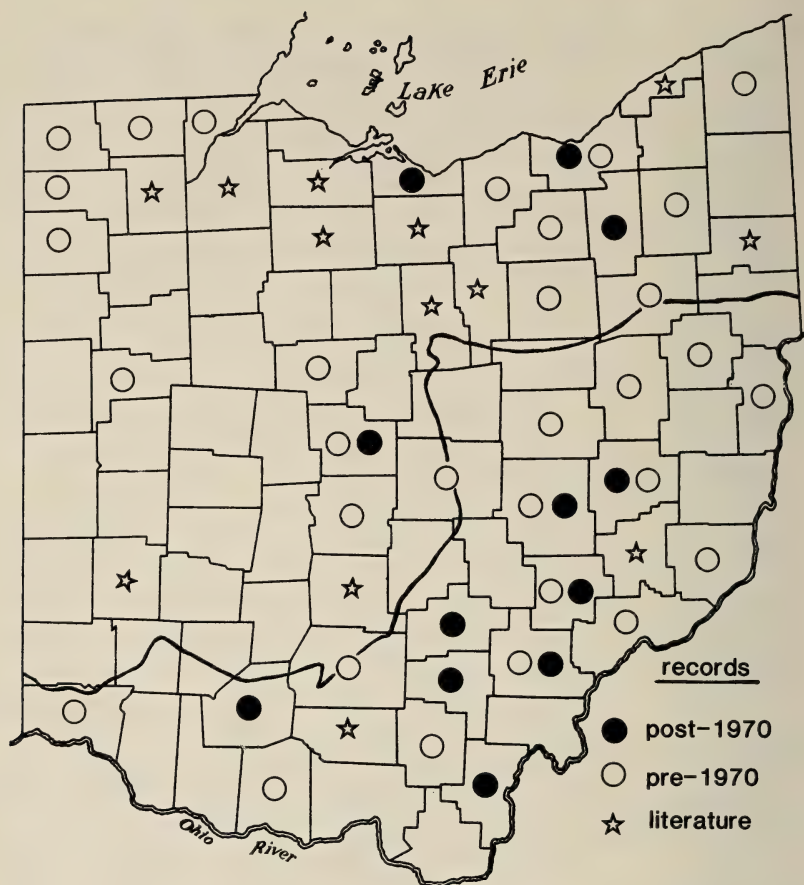
FIG. 2. Distribution of *Speyeria idalia* in Ohio, based on examined specimens and literature records. Line indicates S limit of Wisconsin glacier.

Openings area, very likely as a result of the forestation of the original sandy prairies. Lands in and near the Schwamberger Preserve contain a small population of *samuelis*, but these areas will require intense management if the population of *samuelis* (and other rare butterflies and plants) is to survive.

The Karner blue (and two other rare Ohio butterflies, *Incisalia irus* (Godart) and *Erynnis persius* Scudder) should benefit from habitat manipulations that would increase the local distribution and density of *Lupinus* at the Preserve. Large stands of *Lupinus* currently exist in at least two sites within the Preserve. One site seems ideal for manipulations to establish the plant in the nearby sandy ex-agricultural area. It is likely that prescribed burns could be utilized to enhance the prairie

aspects of the Preserve. *Samuelis* may also benefit from the thinning of shrubby vegetation within the *Lupinus* stands. Recent bulldozing of aspen from land in the Preserve may have inadvertently benefited *samuelis* by removing shade from existing lupine. *Samuelis* was not observed in this area in July 1983, but was frequent in May and July 1984.

Speyeria idalia

Historical distribution. *Speyeria idalia*, the regal fritillary, ranges from N New England W to S North Dakota, S across the N half of the U.S. to E Colorado and Montana (Opler & Krizek 1984). This species was first recorded in Ohio in 1854 (Kirtland 1854). Historically, *idalia* has been most often recorded from the E half of Ohio, although early records indicate it was once common in NW Ohio (Dury 1878, Bubna 1897, Hine 1898a, 1898b, Bales 1909, Henninger 1910, Wyss 1930, 1932). Albrecht (1982) reported that Ohio records include much of the State. It is ironic that there are so few records for *idalia* in the W-central counties of Ohio. This region was once a vast mesic prairie, which should have supported large populations of *idalia*. Perhaps the paucity of records from W-central counties reflects the rapid degradation of *idalia* habitat following conversion of prairies to agricultural land in the mid-1800's, which occurred prior to active collecting in Ohio. In recent years, most collections have been in the SE quarter of the State (Fig. 2).

Habitat and plant associations. The regal fritillary is a butterfly of tall-grass prairie in the Midwest, but is found in other open grassy situations elsewhere. In the East, it is found in damp meadows or pastures with boggy or marshy areas, but it inhabits dry mountain pastures in some areas. The reported primary larval host of *idalia* is bird's foot violet (*Viola pedata* L.); other *Viola* species may be utilized. *Pedata* is extremely rare in SE Ohio (Cusick & Silberhorn 1977), so another violet may be the larval host there. Adults commonly nectar on thistles and milkweeds, along with red clover in pastures.

Current distribution in Ohio. The range of *idalia* in Ohio has apparently diminished in recent years. Most recent records are from SE counties, although there are some records for a few N-central counties since 1970. It has not been recorded in recent years from the NW part of the State. This decline in numbers is not limited to Ohio, as this species appears to have declined precipitously in many areas, and is common only in the few remaining untilled areas in the prairie States (Hammond & McCorkle 1983). In most states, *idalia* is now present only in fragmented populations, and has been extirpated from large regions where it was once common, such as parts of the Ohio Valley and the N Midwest (Opler & Krizek 1984). Its disappearance is likely due to destruction of native prairie habitat, and along with it, destruction of larval host violets.

Discussion. *Speyeria idalia* could probably be preserved in glaciated Ohio by promoting a return of suitable areas to original wet prairie habitats through land purchases or specific land management practices. Presently, this species appears to be unthreatened in unglaciated Ohio. However, it is conceivable that the general decline of *idalia* indicates the future for this species in SE Ohio, and thus its status should be periodically monitored. An effort should be made to determine the larval host plant in SE Ohio.

Phyciodes batesii

Historical distribution. The tawny crescent, *Phyciodes batesii*, ranges from S Quebec and Ontario S to Pennsylvania and Michigan, and W to Nebraska and Colorado. It has

been found in isolated colonies farther S in the Appalachians in Virginia, Kentucky, North Carolina, and Georgia (Opler & Krizek 1984).

All the numerous literature records for this species in Ohio (Bales 1909, Henninger 1910, Wyss 1932, Studebaker & Studebaker 1967) are considered dubious; existing specimens thought to be *batesii* have been determined to be *Phyciodes tharos* (Drury), a common Ohio species.

Habitat and plant associations. In the N part of its range, *batesii* is found in low-lying moist meadows or pastures. In its S distribution, it is found on the tops of dry, rocky bluffs above rivers, or on dry hillsides or rocky upland pastures, usually in association with *Andropogon* grass. The larval foodplant is wavy-leaved aster (*Aster undulatus* L.) and possibly other true asters (Opler & Krizek 1984).

Current distribution in Ohio. There is no evidence that this species currently exists in Ohio.

Discussion. Cusick and Silberhorn (1977) record *A. undulatus*, the known larval foodplant, in 21 of 33 SE Ohio counties. These areas and others where *A. undulatus* is native should be thoroughly explored for *batesii*.

Neonympha mitchellii

Historical distribution. Mitchell's satyr, *Neonympha mitchellii*, displays a disjunct distribution. The only known localities are in New Jersey (Rutkowski 1966), South Carolina, Indiana, Michigan, and Ohio. Midwestern sites occur in a limited area characterized by glacial till topography and calcareous springs.

In Ohio, *mitchellii* was first recorded in Streetsboro Fen in Portage Co. (Pallister 1927) (Fig. 1). Holland (1931) and Macy and Shepard (1941) also cited *mitchellii* in Ohio. Pallister found *mitchellii* abundant in Streetsboro Fen on 4 July 1925 and 10 July 1926. He described the area as a several-hundred-acre peat swamp, but found that *mitchellii* was restricted to approximately one acre of "sedge meadow" surrounded by tamarack and maple. According to McAlpine et al. (1960), *mitchellii* was last reported from the area on 19 June 1950. By 1954, most of Streetsboro Fen had been converted to a truck farm.

Habitat and plant associations. Although the literature reports that *mitchellii* occurs in bogs, all of the habitats described are clearly fens (Shuey 1985) (bog fens in the terminology of Stuckey & Denny 1981). Fens occur over alkaline springs on deposits of peat, and are dominated by sedges (bogs are acidic and are dominated by mosses in the genus *Sphagnum*) (Pringle 1980). Reliable indicators of potential *mitchellii* habitats include tamarack, poison sumac, shrubby cinquefoil and abundant sedges. *Mitchellii* has a strong preference for flying in open stands of tamarack, especially along stream banks.

Mitchellii has been reared on several *Carex* species (McAlpine et al. 1960), but it is not known what species are utilized in the natural habitat. *Mitchellii* is usually closely associated with narrow-leaved *Carex*, probably *C. stricta* Lam. or *C. aquatilis* Wahlenb.

Current distribution in Ohio. Today, there remains little habitat in Ohio resembling the habitats that support viable colonies of *mitchellii* in Indiana and Michigan. Gott Fen State Nature Preserve, located within Streetsboro Fen, is primarily a shrubby cinquefoil meadow, but some limited areas support lush *Carex* openings with which *mitchellii* is associated. *Mitchellii* generally flies in lush sedge meadows adjacent to such areas, but at Streetsboro these are the areas that seem most heavily disturbed. Most sedge meadows in Streetsboro Fen support the broad-leaved sedge, *Carex lacustris* Willd., or rushes, *Scirpus* spp., not the narrow-leaved species with which *mitchellii* is typically associated.

On 29, 30 June, and 6, 7 July 1985, several members of The Ohio Lepidopterists surveyed for *mitchellii* at four fens in Portage Co. (Wingfoot Lake, Mantua Swamp, Frame Lake Bog/Herrick Preserve and Gott Fen State Nature Preserve), one fen in Stark Co. (Timken Bog), and two fens in Summit Co. (Standard Slag Bog and Nimisila Bog

Meadow). *Mitchellii* was not located in these surveys and, because *mitchellii* is usually common when found, and the flight period was well covered in these surveys, it was concluded that *mitchellii* probably is not present at these sites.

Discussion. If *mitchellii* is to be rediscovered in Ohio, efforts should be concentrated in habitats similar to the original Streetsboro Fen. The fen at Herrick Nature Preserve, just S of Streetsboro Fen, lacks suitable sedge meadows, but as far as known, no one has searched Tinkers Creek between these two areas. Many other fens (Mantua Swamp, Kick Fen, others) in NE Ohio fit the general habitat description. Unfortunately, fire suppression has allowed many of these areas to become overgrown with species of dogwood, reducing the amount of suitable sedge meadow. Mantua Swamp and Standard Slag Bog were not completely surveyed in 1985 because of their large size. If sedge meadows occur in the center of these sites, they deserve a closer look. If "new" fens are discovered in the Portage Co. area that contain extensive stands of tamarack, they, too, should be sampled for *mitchellii*.

In NW Ohio, the only likely habitat that remains in undisturbed condition is Mud Lake in Williams Co. *Mitchellii* does not occur at Mud Lake, and probably has not occurred there in recent times (Price 1970). However, Mud Lake is very similar botanically to nearby Cedar Lake fen in NE Indiana, which does support a colony of *mitchellii*.

Catocala marmorata

Historical distribution. The marbled underwing, *Catocala marmorata*, is one of the rarer taxa in the genus. It has not been seen in Ohio since late in the nineteenth century (Dury 1876, 1878, Pilate 1882), and has always been rare over its entire range (Holland 1903, Barnes & McDunnough 1918, Forbes 1954, Sargent 1976). Sargent (pers. comm.) indicated that *marmorata* was collected more regularly in recent years. Collectors in Kentucky have taken about a dozen specimens in the past 10 years; compared to previous years, this would seem a population explosion.

All records for Ohio are from the S half in Hamilton, Montgomery, and Franklin counties (Fig. 3). These records were made by very active collectors (Charles Dury, Cincinnati; George Pilate, Dayton; and W. N. Tallant, Columbus) in the late 1800's. A specimen in the Strecker collection in the Field Museum of Natural History, Chicago, is simply labeled "S. Ohio, 8-26-[18]76". Specimens in the Cincinnati Museum of Natural History and the Field Museum substantiate the historical occurrence of *marmorata* in Ohio. Because this species is not easily confused with others, literature records can be accepted with little hesitation.

Habitat and plant associations. Habitats and plant associations of *marmorata* are unknown. This species is placed with those of the genus whose caterpillars feed on willow and aspen. This placement is supported by overall moth appearance and genitalia (Gall 1984).

Current distribution in Ohio. It is difficult to assess the present status of this species in Ohio. Although it has not been seen in Ohio for approximately 90 years, there have been few active moth collectors in Ohio in that time, and none of them have collected in the SW part of the State where *marmorata* might be found. The species has been collected in an upland oak woods in S Kentucky (Loran Gibson, pers. comm.), but collecting in SW Ohio in similar habitats has not yielded it. *Marmorata* certainly is vagile, and may well have been a temporary resident or even a vagrant in Ohio, as is probably
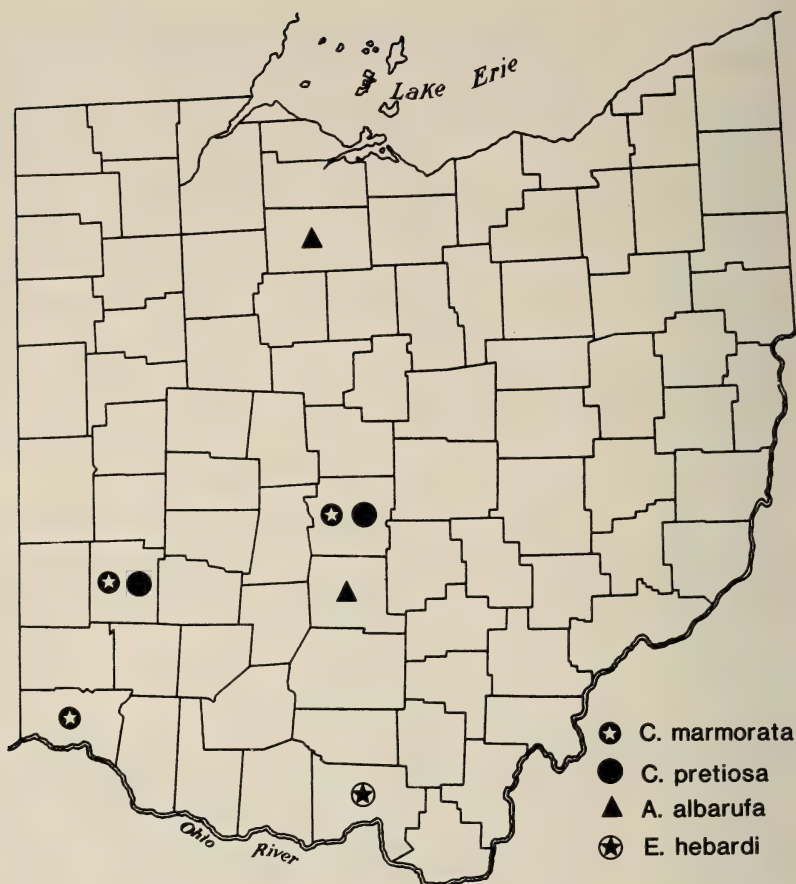
FIG. 3. Distribution of Catocala marmorata, C. pretiosa, Acronicta albarufa, and Erythoecia hebardi in Ohio, based on examined specimens and literature records.

the case for Connecticut, New York, and New Jersey. Given its rarity, *marmorata* might still be found in Ohio.

Discussion. A stronger effort to collect in SW Ohio in willow, cottonwood, and oak habitats is needed. If the supposition is correct that the foodplant is salicacious, wet areas of S Ohio, particularly the SW portion, will be critical to the survival of this species. If, as indicated by some recent captures, the species is associated with oak forests, the concern with wet areas will be lessened. With current environmental emphases on wetlands as habitats, *marmorata* may be protected unwittingly. Land changes affecting other forested areas are more difficult to control.

Catocala pretiosa

Historical distribution. *Catocala pretiosa* has been collected in Ohio several times in Montgomery and Franklin counties (Fig. 3). All collections were made by W. N. Tallant and George Pilate. Pilate and Tallant stopped collecting in Ohio before 1900, when Pilate moved to Georgia, and Tallant moved to Richmond, Indiana; *pretiosa* has not been taken in Ohio since. Extant specimens from Ohio are in the Dayton Museum of Natural History, Dayton, Ohio, the U.S. National Museum of Natural History, Washington, D.C., and the Allyn Museum of Entomology, Sarasota, Florida. Although John and Edward Thomas collected extensively in central Ohio (as well as other areas of the State) in the 1930's, they did not collect *pretiosa*. This is consistent with the distribution reported by Sargent (1976), who states, "This moth was not taken by collectors for many years" (from about 1920 to 1968), and "was often presumed to be extinct". Schweitzer (1982) discussed recent captures of *pretiosa*, and indicated this species may be restricted to southern New Jersey. The New Jersey populations apparently did not exist when *pretiosa* was being collected in other areas, and now that *pretiosa* is being collected in New Jersey, it is unknown in the former locations.

Habitat and plant associations. Schweitzer (1982) reported rearing *pretiosa* on *Prunus maritima* Marsh in New Jersey; also (pers. comm.) that he found one larva on *Pyrus arbutifolia* (L.), red chokeberry, in New Jersey in 1986. Other species in this group of *Catocala* also use *Pyrus* spp. (crabapples), *Prunus* spp. (plums, cherries) and *Crataegus* spp. (hawthorns) as larval host plants. *Prunus maritima* and *Pyrus arbutifolia* do not occur in Ohio; therefore, the larval host in Ohio must be some related plant. If the Ohio foodplant is a species of *Pyrus, Prunus,* or *Crataegus,* the list of possible host species is extensive.

Current distribution in Ohio. Three collecting trips were made in central Ohio (SW Franklin, Madison counties) in late June–early July 1985 to areas with a concentration of possible foodplants. These areas were selected on the basis of the historical distribution of *pretiosa*. General collecting was very good; however, *pretiosa* was not seen.

Discussion. Based on current records and Schweitzer's assumptions, we should not expect to find *pretiosa* in Ohio.

Acronicta albarufa

Historical distribution. *Acronicta albarufa* is recorded from Ohio in only two literature records (Bales 1909, Henninger 1910) (Fig. 3). This species is very similar to *Acronicta ovata* Grote, a common species in Ohio. Without verified specimens from Ohio, it is easy to imagine that the specimens identified as *albarufa* may have been *ovata*. It is not possible to exclude *albarufa* from Ohio's fauna, however, because the reported species range crosses the U.S. from the E coast to New Mexico and Colorado, N to Canada, and S to Georgia (Forbes 1954).

Habitat and plant associations. The apparent habitat requirements of *albarufa* limit the areas where it may be found in Ohio. According to J. G. Franclemont (pers. comm.), the E distribution of *albarufa* is restricted to sandy soils and habitats consistent with "pine barrens" or "sand barrens". Once widespread in the E, according to Franclemont, *albarufa* now seems more confined to coastal areas from New Jersey to Cape Cod, and to pine barrens near Albany, New York. Schweitzer (pers. comm.) has taken *albarufa* at two locations (Ontario and Massachusetts), and states that the moth occurs in the "oak-pine forest on the coastal plain". The oaks are "primarily *Quercus velutina, coccinea, stellata* and *alba* with some *Q. ilicifolia* in the understory". In Massachusetts, where he has collected *albarufa,* Schweitzer reported "The only tree is *Pinus rigida*" with an understory of scrubby oaks that "are well in excess of 99% *Q. ilicifolia*". In Grand Bend, Ontario, Schweitzer collected *albarufa* in a "sandy oak (mostly *Q. velutina*)-pine forest".

Current distribution in Ohio. The oak forests of Ohio have been heavily collected in the past and *albarufa* has not been taken. Three collecting trips were carried out in 1985

in the Oak Openings area of Lucas Co., and the Erie sand barrens in Erie Co. during the known flight period which is May through August. General collecting was good, but no specimens of *albarufa* were seen.

Discussion. Further collecting is needed in suitable habitats, such as the Oak Openings area in Lucas Co., and dry ridge tops of S Ohio. For now, inclusion of *albarufa* as part of Ohio's fauna is tentative.

Erythroecia hebardi

Historical distribution. A population of *Erythroecia hebardi*, one of the rarest moths in North America, occurs in Scioto Co., Ohio (Fig. 3). The size of the Ohio population is unknown. Originally described in 1917 from two specimens from Hot Springs, Virginia, *hebardi* has not been seen from Virginia since. Until 1984, all known specimens, except the types, have come from N-central New Jersey, near Lake Hopatcong and Johnsonburg. Before 1984, fewer than 10 specimens were known in collections. Of these, only two, those from Johnsonburg, are recent records; all others predate 1930. Nothing is known of the life history, and only guesses can be made about its habitat requirements.

This species was first collected in Ohio at UV light on 26 August 1984 in Shawnee State Forest, Scioto Co. The site was a clearing that resulted from a recent clearcutting. More collecting in 1985 and 1986 yielded additional specimens, several of which came from two additional locations, 1.2 km and 4.2 km S of the first site. The second and third sites are also recent clearcuts.

Habitat and plant associations. In all occurrences of this moth in Ohio, the habitat is a recent clearcut area in mature second growth forests in the rugged unglaciated Allegheny Plateau of the S part of the State. This is an area of steep hills capped with sandstone ridges, and acidic, dry soils. Common forest trees are upland mixed oaks, hickories, maples, native pines (Virginia, yellow, and pitch), and yellow poplar. Usual forest groundcover plants are several kinds of blueberries, huckleberries, and other members of the heath family. Because of the acidic soils, diversity of wildflowers is low (King 1979).

Adventive species of plants such as clovers, sunflowers, goldenrods, ragweeds, etc., quickly invade the clearcut areas to provide considerable diversity of plants not found in the forest. All specimens of *E. hebardi* collected so far have come from clearcut areas immediately adjacent to the forest. Larval foodplant and habitat requirements are unknown.

Current distribution in Ohio. To date, this species has been collected only in Scioto Co., in S Ohio.

Discussion. Based on information gathered to date, the continued survival of *hebardi* in Ohio is encouraging. More complete information pertinent to its habitat and food requirements is essential. The occurrence of *hebardi* in Ohio provides a unique opportunity for research to discover reasons for its previous rarity.

CONCLUSIONS

Most of the species discussed indicate unique ecological situations in Ohio. Further investigation into the ecological requirements of all the species and their habitats is warranted. The presence of populations can and should be used in decisions concerning the preservation of unique and endangered habitats. Special emphasis should be placed on *Lycaeides melissa samuelis* and *Erythoecia hebardi* because both are limited to very small geographic areas in Ohio; survey work should be

directed toward locating additional populations of these species. *Speyeria idalia* seems secure in unglaciated Ohio, but further research is needed to determine larval host plants and the reasons for population fluctuations. On the other hand, this species has declined in glaciated areas. Conservation efforts for this species should therefore be concentrated on the isolated populations in glaciated Ohio. There should be a continuing effort to locate *Phyciodes batesii*, *Neonympha mitchellii*, *Catocala marmorata*, *Catocala pretiosa* and *Acronicta albarufa* in Ohio.

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MILKWEED PATCH QUALITY, ADULT POPULATION STRUCTURE, AND EGG LAYING IN THE MONARCH BUTTERFLY

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ABSTRACT. Relations between hostplant patch attributes (patch size, plant density, plant age, nectar availability), adult population structure (population size, sex ratio, age structure), and measures of egg laying (number of eggs per plant, total number of eggs per patch) in *Danaus plexippus* (L.) and its hostplant *Asclepias fruticosa* L. were investigated. Sex ratios were male biased in areas with high hostplant density (patches), and female biased in nonpatch areas. Numbers of eggs per plant were higher on single, isolated plants (areas of low hostplant density) than on patch plants. Relations between adult population attributes and measures of egg laying were not clear-cut. Contrary to expectations, neither nectar availability nor sex ratio influenced measures of egg laying. Patch size and number of females in a patch were also unrelated to total number of eggs in a patch. However the last was positively related to number of males and percentage of young females in a patch, and negatively correlated with percentage of young males in a patch.

Additional key words: *Danaus plexippus*, Nymphalidae, *Asclepias fruticosa*, Australia.

Boggs and Gilbert (1979) demonstrated that mating provides not only sperm but also nitrogen-rich nutrients for egg production by females in the monarch butterfly, *Danaus plexippus* (L.), and two heliconid species. This nutritional contribution may be most important in multi-mating species which produce large spermatophores, such as *D. plexippus* (Burns 1968, Pliske 1973, Suzuki & Zalucki 1986). Bull et al. (1985) and Suzuki and Zalucki (1986) showed experimentally that female *D. plexippus* are more likely to remain in and around patches of the milkweed *Asclepias fruticosa* (L.) where the sex ratio [males/(males and females)] is greater than 0.5. This implies that males are a major limiting resource for females.

Many factors in addition to males influence egg laying on hostplants, including species, size, age, and condition of the plants (Zalucki & Kitching 1982a). Egg laying in patches of plants is further influenced by patch size, rules of female movement (Zalucki & Kitching 1982a, 1982b, Zalucki 1983), and female age (Zalucki 1982). In this study, we looked for relations among monarch population attributes around patches (population size, sex ratio, age, and distribution), patch characteristics (size, plant density and age, nectar availability) and egg "investment" (number of eggs per plant, total number of eggs per patch), after

TABLE 1.   Effect of patch category on sex ratio (proportion male) in two sampling periods.

	Sampling period					
	24–31 Aug. 1983			20 Feb.–1 Mar. 1984		
Patch category	No. of patches	Mean ± SD sex ratio	Range of sex ratios	No. of patches	Mean ± SD sex ratio	Range of sex ratios
Nonpatch	4	0.38 ± 0.11	0.24–0.50	4[a]	0.43 ± 0.03	0.40–0.47
Small	8	0.54 ± 0.10	0.35–0.66	7	0.61 ± 0.09	0.43–0.69
Medium	1	0.63	—	4	0.65 ± 0.07	0.58–0.72
Large	2	0.46 ± 0.01	0.45–0.47	2	0.61 ± 0.08	0.55–0.67

[a] Excludes 1 misclassified nonpatch.

recording these attributes from a large and diverse sample of milkweed patches over a short duration.

MATERIALS AND METHODS

Milkweed patches were sampled on two occasions giving a total of 33 patches. During the first sampling period (24 to 31 August 1983), monarchs in and very near 15 patches were netted for 1 person h at each patch. All butterflies caught were sexed and scored for age on the basis of wing condition as follows: A'—wing soft, A—wings intact, B—wings frayed, C—wings very frayed. In this first survey, patches were classified subjectively: nonpatch (milkweed scattered and at very low density, <1 plant/m^2), small patch, medium, or large patch. Egg numbers were not recorded. This survey could be used only to ascertain relations between patch category and butterfly sex ratio. Patches were located in and near Beenleigh (27°43'S, 153°12'E), Logan Village (27°46'S, 153°06'E), and Mt. Crosby (27°32'S, 152°42'E) in SE Queensland, Australia.

On the second sampling occasion (20 February to 1 March 1984), 18 patches located along the Kenmore (27°30'S, 152°56'E)–Mt. Crosby Road were used. Adults were netted for 1 person h per patch, sexed, and aged as before. An attempt was made to estimate adult sampling efficiency. In smaller patches it is easier to obtain a high sampling fraction than in large patches. Sampling fractions were estimated subjectively on the basis of butterflies seen after netting ceased. Sampling fraction is the ratio of butterflies caught in 1 person h to butterflies caught plus those seen flying at the end of netting. Patch size was measured by idealizing the patch to standard shapes (circle, square, etc.) and recording relevant distances using a tape measure. Plant density within a patch was estimated using 6 to 25 randomly thrown 1-m^2 quadrants. From each patch a sample of ca. 100 plants was selected, cut at ground level, placed in plastic bags, and returned to the labo-

TABLE 2.   Details of sampling during 20 February–1 March 1984.

Date	Starting time (h)	Temperature range (°C)	Remarks	Patch category*	Sex ratio	Sampling fraction
20-2-84	0945	21–29	Cloudy,	3	0.69	0.80
	1045		showers	2	0.69	0.80
21-2-84	0855	22–30	Cloudy,	2	0.66	0.70
	0950		fine	1	0.47	0.30
	1040			3	0.72	0.70
	1145			2	0.69	1.00
22-2-84	0910	22–27	Cloudy	2	0.56	0.70
	1000			4	0.55	0.30
	1100			3	0.61	0.80
23-2-84	0910	21–29	Cloudy,	3	0.58	0.60
	1000		showers	2	0.43	0.30
	1055			4	0.67	0.70
28-2-84	0935	22–36	Fine	2	0.67	0.30
	1015			1	0.43	0.80
	1100			2	0.67	0.60
1-3-84	0900	20–27	Cloudy	2	0.59	1.00
	0945			1	0.44	0.70
	1035			1	0.43	0.80

* 1 = nonpatch; 2 = small patch, <20,000 plants; 3 = medium patch, 20–80,000 plants; 4 = large patch, >80,000 plants.

ratory. These were measured and classified as young, with flowers, with small pods, with old pods, or dead. They were then searched for eggs and larvae. Percentage of flowering milkweed plants provided an estimate of nectar availability. Other potential nectar resources (lantana, weeds) were scored subjectively as low, medium, or high.

RESULTS

Data from both sampling periods were combined to look for relations between patch category and sex ratio (Table 1). A two-way ANOVA on an arcsin (square root) transformation (Sokal & Rohlf 1981) indicated highly significant effects of patch category ($P < 0.001$) and sampling period ($P < 0.05$). However, removing the nonpatch category from analyses removed the effects of both patch category ($P > 0.05$) and sampling period ($P > 0.05$) on sex ratio. Nonpatches had consistently female-biased sex ratios (Table 1) whereas patches, regardless of size, had variable but generally male-biased sex ratios (Table 1).

More detailed observations were made during the second sampling period. Neither time of day nor weather had any obvious effect on sex ratios or sampling fractions (Table 2). Sampling fraction is a function of patch size and terrain. Smaller sampling fractions were recorded for large patches and for patches on hillsides or with long grass.

Relations between various measures for eggs laid, patch, and butterfly

TABLE 3. Correlation matrix for all variables in 13 patches. Only coefficients significant at P < 0.05 are shown. * indicates significance due to one or two outlying points.

Variable label		X1	X2	X3	X4	X5	X6	X7	X8	X9	X10	X11	X12	X13	X14
Patch size	X1														
Plant density	X2	0.87													
Total no. plants[a]	X3														
% flowering	X4														
Other nectar	X5														
Plant age	X6			0.50											
No. eggs/plant	X7		-0.53												
No. ♂[b]	X8	0.67	0.48	0.90			0.53	-0.55							
No. ♀[b]	X9	0.65	0.49	0.84*			0.51		0.90						
Total no.	X10	0.68	0.50	0.89*			0.53	-0.52	0.98	0.97					
Sex ratio	X11														
% young ♂	X12	-0.53								-0.60*					
% young ♀	X13							0.57*							
Total no. eggs[c]	X14	0.85		0.88					0.74*	0.68*	0.73		-0.65		

[a] (Patch size, m²) × (no. plants/m²).
[b] Corrected for sampling fraction.
[c] (Total no. plants) × (mean no. eggs/plant).

Eggs/plant (×100)
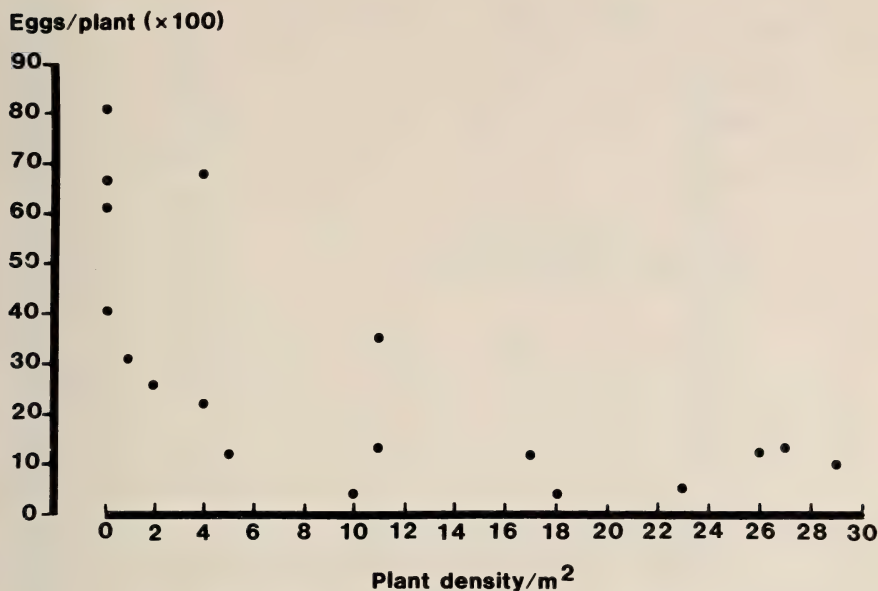
FIG. 1.   Effect of plant density on number of eggs per 100 plants. Points with plant density 0 correspond to nonpatches.

variables were compared using all possible pairwise correlations, ignoring nonpatches. The correlation matrix (Table 3) shows only coefficients significant at $P < 0.05$ (one-tailed t-test). Some correlations were "significant" due to one or two outlying points. These relations are probably superficial.

A number of patterns are apparent in Table 3. Patch-size variables (area and total number of plants in patch) and numbers of adult butterflies were positively correlated with total numbers of eggs in patches. However, numbers of eggs per plant were negatively related to plant density (Fig. 1) and patch size. Plant age (% plants with pods and dead stems) correlated positively with numbers of butterflies, but this may follow from the positive association between total numbers of plants and plant age.

One striking result was that neither number of females nor percentage of young females in a sample had any influence on total number of eggs or number of eggs per plant, respectively, once outlying points were removed. Equations for these relations are: Total no. eggs (y) = $167 \times$ No. females (x) + 1,775, $F_{1,11} = 9.493$, $P < 0.05$ when all points included; deleting one outlier, y = 25x + 4,177, $F_{1,10} = 0.079$, $P > 0.05$; and No. eggs/plant (y) = $0.57 \times$ % young females (x) − 1.87, $F_{1,11} = 5.277$, $P < 0.05$ when all points included; deleting two outliers, y = 0.091x + 10.16, $F_{1,9} = 0.144$, $P > 0.05$).

TOTAL EGGS (× 100)
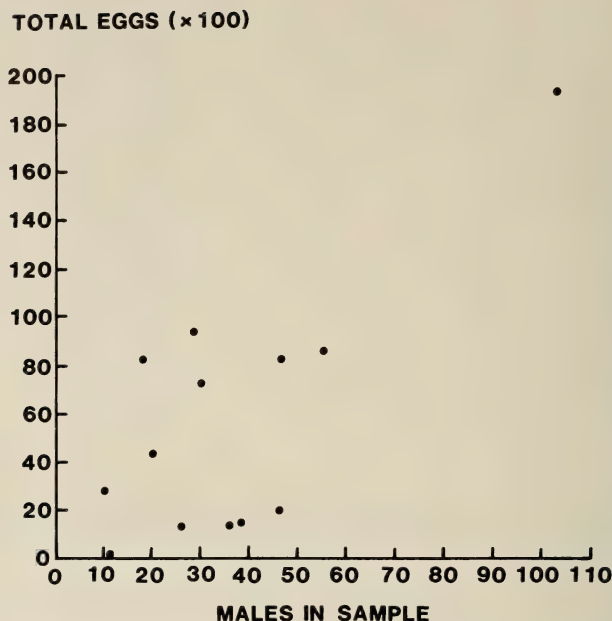
FIG. 2.   Effect of number of males caught on total number of eggs in a patch.

On the other hand, number of males in a sample had a negative association with number of eggs per plant, a positive one with total number of eggs (Fig. 2), and the latter was negatively related to percentage of young males in a patch (Fig. 3). The positive association between number of males (x) and total number of eggs (y) was significant ($P < 0.05$) only if all points were included (Fig. 2, $y = 158x + 37.8$, $F_{1,11} = 13.62$). Deleting the extreme value from this figure removes significance ($y = 67.39x + 2,585$, $F_{1,10} = 0.8958$, $P > 0.3$). This was not the case for the relation between total number of eggs (y) and % young males (x) (Fig. 3). Removing one or two extreme values did not change this relation (with the two extreme left-hand points deleted, $y = -295.7x + 17,676$, $F_{1,9} = 5.728$, $P < 0.05$). The negative association of number of eggs per plant and number of males probably stems from the negative relations of number of eggs per plant to total plant number and density, and the strong positive association between these variables and male number (Table 3). Neither nectar availability nor sex ratio influenced adult numbers or measures of egg laying.

For any set of data where most variables are correlated and interdependent, single pairwise comparisons may be misleading. From the above analysis the variables total number of eggs in a patch, patch size, numbers of males and females, and percentages of young males and

TOTAL EGGS (×100)
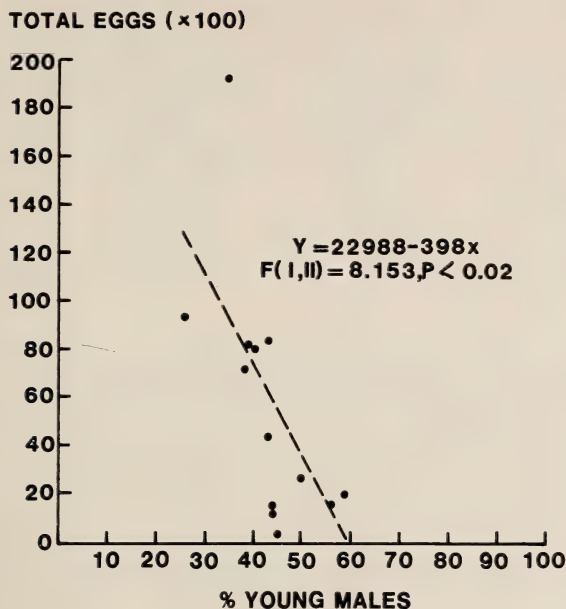
FIG. 3. Relation of percentage of young males to total number of eggs in a patch.

females in a patch were entered in a partial correlation matrix (Table 4). Total number of eggs in a patch was positively correlated with male density, but negatively correlated with percentage of young males in the population. Total number of eggs laid and percentage of young females were also positively related (P < 0.10), as was egg number and percentages of young males and females (P < 0.05). Surprisingly neither patch size nor number of females was related to total number of eggs laid.

These analyses were corroborated by stepwise linear regression with total number of eggs as the dependent variable. Results (Table 5) indicated significant effects only for number of males, % young males, and % young females.

DISCUSSION

Zalucki and Kitching (1985) and Bull et al. (1985) found that sex ratios tend to be male-biased in and around milkweed patches. If, as they suggest, male bias cannot be explained by sex ratio at birth, survival difference, or sampling bias within a patch, then where do the females go? The present study confirms male bias around milkweed patches (ca. 60%) and demonstrates a female-biased population outside patches (nonpatch areas), hilltops notwithstanding. As with many Lepidoptera

Table 4. Partial correlation matrix for selected patch, butterfly, and egg-laying variables.

| | Total eggs X1 | Patch size X2 | Number | | % young | |
			Males X3	Females X4	Males X5	Females X6
x2	0.52					
x3	0.72**	−0.17				
x4	−0.37	0.24	0.80**			
x5	−0.79**	0.13	0.69**	−0.40		
x6	0.62*	−0.10	−0.52	0.20	0.60*	

** $P < 0.01$; * $P < 0.05$.

(Shields 1967, Parker 1978, others) male monarchs can be taken in numbers around hilltops.

The egg-laying pattern found by Zalucki and Kitching (1982a) on artificial milkweed "patches" was also confirmed by this study. Number of eggs per plant was much higher on single isolated plants than on patch plants (Fig. 1). This result can be explained in part by how female monarchs search for and use a host plant (Zalucki & Kitching 1982b, Zalucki 1983), and by female-biased sex ratios outside patches (single plants). Jones (1977) found a similar pattern of egg-laying in *Pieris rapae* (also see Shapiro 1981, Thompson & Price 1977, Wiklund & Ahrberg 1978). However, there are many alternate explanations for such a pattern (Mackay & Singer 1982).

Within patches, relations among patch and butterfly variables and measures of egg-laying are not straightforward. Contrary to expectation, sex ratio was not related to any measure of egg-laying. Nor was number of eggs in a patch related to availability of nectar, number of females in a patch, or patch size (Tables 3–5). Bull et al. (1985) and Suzuki and Zalucki (1986) showed experimentally that female residence time in a patch is positively related to sex ratio, and Bull et al. (1985) could not find any effect of butterfly density on residence time. Neither study recorded egg numbers in experimental patches.

In the present study, number of eggs in a patch was positively related to number of males (all ages), but not to number of females, even though the latter two variables are strongly positively associated (Tables 3, 4). This provides further circumstantial evidence that males are a major "egg-laying resource" for females through provision of nutrients as well as sperm at mating (Boggs & Gilbert 1979, Suzuki and Zalucki 1986). Also, Herman and Barker (1977) showed that mating stimulates oogenesis. There was a weak positive relation between female age structure and number of eggs; patches with a high percentage of young females had more eggs. This presumably reflects the high fecundity of such females (Zalucki 1982).

TABLE 5. Stepwise linear regression of total number of eggs against patch size, number of males and females, and % young males and females.

Independent variable	Coefficient (±SE)	Standardized Coefficient	*t*-value	P
Patch size	18.88 (11.67)	0.28	1.618	NS
No. males	153.40 (55.54)	0.72	2.762	**
No. females	−65.18 (61.35)	−0.27	−1.062	NS
% young males	−271.40 (80.34)	−0.44	−3.379	**
% young females	69.16 (33.21)	0.23	2.083	*

** P < 0.05; * P < 0.10.

In contrast, number of eggs in a patch was inversely related to percentage of young males in the population. Are young males more aggressive (inexperienced) in courtship and do they subsequently "drive" females from a patch? This hypothesis will require further testing.

ACKNOWLEDGMENTS

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ANNOUNCEMENT

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William E. Miller, Editor

HOST SPECIFICITY AND BIOLOGY OF *BUCCULATRIX IVELLA* BUSCK, A POTENTIAL BIOLOGICAL CONTROL AGENT FOR *BACCHARIS HALIMIFOLIA* L. IN AUSTRALIA

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ABSTRACT. Life history and host range of *Bucculatrix ivella* were investigated as part of a program to find host-specific biocontrol agents for *Baccharis halimifolia* in Australia. This multivoltine insect was collected on *B. halimifolia* and *B. neglecta* from Texas to New Jersey. Though usually found at low population densities, it occasionally occurred in numbers sufficient to defoliate plants. Host specificity tests of oviposition preference and larval feeding indicated that *B. ivella* was specific to *Baccharis* species. These tests and a field survey indicated that *Iva frutescens* is definitely not a host although it is reported as such in the literature. *Bucculatrix ivella* has been approved for introduction into Australia for the control of *B. halimifolia*.

Additional key words: Lyonetiidae, *Baccharis neglecta*, *Iva frutescens*, introduction, weed.

Following its introduction into Queensland, Australia, before 1900, the North American shrub *Baccharis halimifolia* L. (Asteraceae: Astereae: Baccharineae) has become a serious weed in SE Queensland and NE New South Wales by invading pastures and land cleared for reforestation. The plant was declared noxious in 1951; subsequently a biological control program to find and introduce suitable host specific insects from the New World was implemented. This program consisted of intensively surveying appropriate areas, selecting stenophagous species from available knowledge, testing the host range of these species experimentally and, if their host range was limited to *Baccharis*, mass rearing and releasing in Australia.

One such candidate from the surveys of the fauna on *B. halimifolia* and *B. neglecta* Britt. (Palmer 1987, Palmer & Bennett, in prep.) was the leafminer *Bucculatrix ivella* Busck. This insect was first reported on *Iva frutescens* L. (Busck 1904), but since has been reported only from *B. halimifolia* (Braun 1963, R. W. Hodges, pers. comm.). However, we suspected the host record on *I. frutescens* may have been in error when another species, *Aristotelia ivella* Busck (Gelechiidae), collected by H. Dyar from the same plants (Busck 1904) proved to be specific to *Baccharis*.

The genus *Bucculatrix* is cosmopolitan with about half the species found in America north of Mexico. Braun (1963) described 99 species, including 50 new species, that occur in this region. Little taxonomic work has been done on the genus since, and there are undoubtedly many undescribed species (R. W. Hodges, pers. comm.). Although the known food plants include 25 plant families, nearly ⅔ of *Bucculatrix* species were associated with Asteraceae, and more than ¾ were recorded from a single plant genus (Braun 1963). Braun (1963) listed three pest species: *B. thurberiella* Busck, *B. canadensisella* Chambers, and *B. pomifoliiella* Clemens, which attack cotton, birch, and apple, respectively. An undescribed *Bucculatrix* has already been released in Australia for control of the weed *Parthenium hysterophorus* L.

At least four species are associated with *Baccharis*. In addition to *Bucculatrix ivella*, *B. separabilis* Braun, and *B. variabilis* Braun are associated with *Baccharis pilularis* DC. in California (Braun 1963). Recently, we collected an undescribed species from *B. sarathroides* Gray in Arizona.

This paper reports results of experimental and field observations undertaken to investigate the host specificity of *Bucculatrix ivella*. In the course of the study, biology and phenology of *B. ivella* were observed and are also reported.

BIOLOGY

The biology of *B. ivella* is typical of leaf-mining species of *Bucculatrix* described by Braun (1963). The following description is based on numerous laboratory and field observations of life stages. Eggs were whitish, translucent, and flatish ovoid in shape, and were cemented to the leaf surface, usually along the upper surface of the midrib of the leaf. In sunlight they had a characteristic iridescence and were thus easily recognized.

Larvae hatched within 7–11 days and entered the leaf tissue directly where they mined the parenchyma. Mines were distinctive threadlike tracks which initially followed a leaf vein but eventually became irregular, serpentine, and black with the deposition of frass. Larvae spent the first, second, and part of the third instars in these mines. After leaving the mines, they spun flat, thin "molting cocoons" under which they molted. Fourth and fifth instars were external feeders, and a second "molting cocoon" was formed at the end of the fourth instar. Larvae were found on either upper or lower leaf surfaces, although the latter were more commonly infested. When disturbed, larvae dropped on a silken thread. They consumed leaf tissue in patches but left the opposite epidermal tissue intact, which produced a "window" effect.

TABLE 1.   Number of plants infested with *Bucculatrix ivella* after exposure in a glasshouse.

Plant species (Tribe)	Number examined	Number infested
Baccharis halimifolia L. (Astereae)	3	2
B. neglecta Britton (Astereae)	5	2
B. glutinosa (R. & P.) (Astereae)	1	0
B. pilularis DC. (Astereae)	1	0
Solidago altissima L. (Astereae)	1	0
Haplopappus tenuisectus (Green) Blake (Astereae)	2	0
Aster novae-angliae L. (Astereae)	2	0
Conyza canadensis (L.) (Astereae)	1	0
Iva frutescens L. (Heleantheae)	10	0
Leucanthemum maximum Ramond (Anthemideae)	5	0
Ageratum houstonianum Mill. (Eupatoreae)	2	0

Pupation occurred within characteristic ribbed cocoons spun on leaves and stems of *Baccharis*. However, when larvae were abundant, some left the host to pupate on neighboring plants or in ground debris.

Before eclosion, the pupa thrust through the anterior end of the cocoon, exposing about half its length. Pupal cases remained attached to cocoons after moth emergence. Moths remained quiescent on foliage during the day and became active at dusk.

HOSTS, DISTRIBUTION AND PHENOLOGY

Bucculatrix ivella has been collected nearly throughout the range of *Baccharis halimifolia*; we collected it in New Jersey, Virginia, Florida, Louisiana, and Texas. In Texas, the immatures were most abundant in late April and early May, when infested plants had 50–100 larval mines, but after early spring few individuals were seen. In Florida, the life cycle was completed in 4–6 weeks and larvae were found at most times of the year. Several hundred mines per plant were observed in Virginia and New Jersey in June and July, and these populations caused severe defoliation. It is perhaps the most abundant lepidopteran associated with *B. halimifolia*.

In central Texas, *Bucculatrix ivella* was collected from *Baccharis neglecta*, which is a new host record. However, natural populations on this species were invariably low, even though it breeds readily on this plant under glasshouse conditions.

Collections of *Bucculatrix ivella* immatures invariably contained a proportion (10–90%) of parasitized specimens. Among the parasites to emerge were species of the hymenopterans *Ageniaspis* (Encertidae), *Apanteles* (Braconidae), *Bucculatriplex* (Braconidae), *Cirrospilus* (Eulophidae), *Mirax* (Braconidae), *Opius* (Braconidae) and *Tetrastichus* (Eulophidae).

TABLE 2.   Degree of infestation by *Bucculatrix ivella* on six plants in an unreplicated cage experiment.

Plant species (Tribe)	Infestation
Baccharis halimifolia L. (Astereae)	13 larval mines
	20 larval cocoons
	5 late instars
	external feeding damage
	>60 pupal cocoons
Aster novae-angliae L. (Astereae)	none
Solidago altissima L. (Astereae)	none
Callistephus chinensis (L.) Nees (Astereae)	none
Cynara scolymus L. (Cardueae)	none
Iva frutescens L. (Heleantheae)	none

HOST SPECIFICITY

Host specificity was determined by laboratory trials and field observations designed first to demonstrate whether *Iva frutescens* in particular, and Asteraceous plants in general, were hosts, and second, to test the insect against a wide variety of plants of economic importance to Australia.

Field observations. In Virginia and New Jersey, *Baccharis halimifolia* heavily infested with *Bucculatrix ivella* was found growing close to *Iva frutescens*. Sometimes the branches of the two intertwined. *Iva frutescens* was carefully searched without ever finding an infestation of *Bucculatrix ivella*.

The area where the report on *Iva frutescens* originated (Palm Beach, Florida) was also searched. However, *I. frutescens* was not found there; it is apparently rare S of Daytona Beach, Florida, while *Baccharis halimifolia* is common.

Larval feeding. On four occasions over a two-year period, late instars were collected from *B. halimifolia* and returned to the laboratory where 5 to 10 were placed on bouquets of *B. halimifolia* and *I. frutescens*. Larvae invariably continued feeding and pupated on the *B. halimifolia*, but no evidence of feeding was found on the *I. frutescens*.

Glasshouse observations. Potted asteraceous plants were introduced into a glasshouse containing potted *Baccharis* plants infested with *Bucculatrix ivella*. After two months, the plants were carefully examined for infestations of *B. ivella*. Only *Baccharis halimifolia* and *B. neglecta* were infested (Table 1).

Cage experiment. A cage experiment was conducted in a glasshouse using *B. halimifolia* and five other asteraceous species common in Australia. One potted plant of each species was placed in a wooden cage with a clear plastic top. Thirty pupae and four moths were introduced together with four sugar-water wicks. When the *B. halimifolia* plant was infested, all plants were removed and carefully examined. A number of infestations were found on the *B. halimifolia*, but none of the other plants was infested (Table 2).

Comprehensive testing. Before permission to release the insect in Australia could be sought, *Bucculatrix ivella* had to be tested against the complete list of plants suggested by the Commonwealth Department of Health (Table 3). Oviposition preference was tested using a $5.0 \times 4.5 \times 3.0$ m glass-sided cage into which were randomly placed young, actively growing tip cuttings of all test plants and *Baccharis halimifolia*. These cuttings were held in glass vials with water. Twenty moths were placed in the cage together with a honey-water mixture. After 6 days, when the *B. halimifolia* was infested with eggs, the cuttings were carefully examined and any eggs counted. After a further six days, when larval mines were seen in *B. halimifolia* leaves, the cuttings were reexamined for eggs or mines. The experiment was replicated twice. Numbers of eggs and larval mines were seen on all *B. halimifolia* cuttings, but not on any other cutting.

In a second experiment, host range of the ectophagous late instars was tested. Five fourth or fifth instars collected from the field were placed on two potted plants of each

TABLE 3.   Plant species against which *Bucculatrix ivella* was tested to obtain permission for its introduction into Australia.

Apiaceae: *Daucus carota* L.; *Pastinaca sativa* L.
Anacardiaceae: *Mangifera indica* L.
Asteraceae: *Baccharis halimifolia* L.; *Carthamus tinctorius* L.; *Chrysanthemum* sp.; *Dhalia* sp.; *Helianthus annuus* L.; *Lactuca sativa* L.
Brassicaceae: *Brassica oleraceae* (L.) Alef.; *Brassica rapa* L.
Bromeliaceae: *Ananas comosus* (L.) Merr.
Caricaceae: *Carica papaya* L.
Chenopodiaceae: *Beta vulgaris* L.
Convolvulaceae: *Ipomoea batatas* (L.) Lam.
Cucurbitaceae: *Cucumis melo* L.; *Cucumis sativus* L.; *Curcubita maxima* Duch.
Fabiaceae: *Arachis hypogaea* L.; *Centrosema pubescens* Benth.; *Desmodium canum* (Gmel.); *Glycine wightii* (R. Grah. ex Wight & Arn.) Verdc.; *Glycine max* (L.) Merr.; *Medicago sativa* L.; *Phaseolus atropurpureus* DC.; *Phaseolus vulgaris* L.; *Pisum sativum* L.; *Stizolobium* sp.; *Stylosanthes gracilis*; *Trifolium repens* L.; *Vigna catjang* V.
Linaceae: *Linum usitatissimum* L.
Malvaceae: *Gossypium hirsutum* L.
Mimosaceae: *Leucaena leucocephala* (Lam.) de Wit.
Musaceae: *Musa sapientum* M.
Passifloraceae: *Passiflora edulis* Sims
Pinaceae: *Pinus radiata* D. Don.; *Pinus taeda* L.
Poaceae: *Avena sativa* L.; *Digitaria decumbens* Stent.; *Panicum maximum* Jacq.; *Paspalum dilatatum* Poir.; *Pennisetum clandestinum* Chiov.; *Saccharum officinarum* L.; *Sorghum vulgare* L.; *Triticum aestivum* L.; *Zea mays* L.
Proteaceae: *Macadamia integrifolia* Maid & Betche
Rosaceae: *Fragaria vesca* L.; *Malus sylvestris* Mill.; *Prunus domestica* L.; *Prunus persica* (L.) Batch.; *Pyrus communis* L.; *Rosa* sp.
Rutaceae: *Citrus limon* (L.) Burm. F.; *Citrus paradisi* Macfady.; *Citrus reticulata* Blanco; *Citrus sinsensis* (L.)
Sapindaceae: *Litchi chinensis* Sonn.
Solanaceae: *Capsicum annuum* L.; *Lycopersicum esculentum* Miller; *Nicotiana tabacum* L.; *Solanum tuberosum* L.
Vitaceae: *Vitis vinifera* L.
Zingiberaceae: *Zingiber officinale* Roscoe.

species, which were observed for 10 days. Larvae on all plants other than *B. halimifolia* were seen leaving the plants in the first two days, and no feeding was attempted on them. On the other hand, all larvae on *B. halimifolia* were seen to feed normally.

DISCUSSION

The tests conducted on *Bucculatrix ivella* clearly showed its specificity to some species of *Baccharis* such as *B. halimifolia* and *B. neglecta*; also that *Iva frutescens* was not a suitable host. The most likely explanation for the record on *I. frutescens* is that *B. halimifolia* was misidentified as that species. The two are morphologically similar and grow in similar habitats. They are both known by the same common name, "salt bush". A second explanation is that if the two plant species were growing together, late instars could have migrated onto the *I. frutescens*

to pupate. This is less likely because *I. frutescens* does not grow, or is rare, in Palm Beach Co., Florida, where the collection was made.

Bucculatrix ivella has considerable potential as a biocontrol agent and is also relatively easy to rear and handle in the laboratory. It is multivoltine and capable of building up to high populations that greatly damage the plant. In North America, it is heavily parasitized, but before release in Australia it will be freed of parasites. In the absence of parasites, the rate of population growth in Australia should be greater than in its native habitat.

Permission to import this insect into Australia was granted in 1986.

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BUTTERFLIES FROM THE UJUNG KULON NATIONAL PARK, INDONESIA

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ABSTRACT.   Butterflies found on the Ujung Kulon Peninsula (85 spp.) and Pulau Peucang (36 spp.) in 1984 are listed and compared with the fauna of the Krakatau Islands. Many species are limited to particular vegetation types or ecotones, and maintenance of habitat diversity appears vital to ensure continued diversity in the national park. At present, management for grazing by large mammals and limited human access are practical conservation measures for butterflies.

Additional key words: Java, surveys, conservation, biogeography.

The Ujung Kulon Peninsula and adjacent islands comprise the westernmost region of Java, Indonesia. Since the large-scale inundations by tsunamis associated with the eruption of Krakatau in 1883, this region has been largely free from human activities. It is now a national park to which access is strictly controlled and monitored, and in which scientific work may be undertaken only by permit. Land access is difficult, and most visitors arrive by boat from towns on the NW coast of Java and stay predominantly on Pulau Peucang (Fig. 1). The main purpose of this park, which comprises some 30,000 ha, is to foster the last remaining population of the Javan rhinoceros, *Rhinoceros sondaicus sondaicus* Desmarest, but the relatively undisturbed forest and other vegetation types render it one of the most significant areas in Java for the conservation of native fauna. Much of the forest survived the 1883 catastrophe, but little forest now present is considered to be true mature lowland rainforest (Blower & van der Zon 1977). The latter occurs on Gunung Payung, the highest point of the western part of the park, and on the nearby island of Pulau Peucang (Fig. 1). Much of the rest of western Java has undergone considerable change in support of a burgeoning human population, and there is little doubt that the Ujung Kulon National Park now harbors remnant populations of many taxa

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which were formerly much more widespread. In common with much of the "third world", the distribution of reserves tends to reflect human settlement patterns, but the significance of Ujung Kulon was recognized by bestowal of the status of "nature reserve" in 1921 (Hoogerwerf 1970). Since that time it has been upgraded to a national park, and Ujung Kulon has become "the most widely known conservation area in South East Asia" (Blower & van der Zon 1977). It assumes additional biogeographical importance as a likely major source area of animals and plants that have reached the Krakatau Islands over the last century since life there was expunged in 1883.

In 1984, La Trobe University and the Bogor Zoological Museum mounted a joint expedition to survey the fauna of the Krakatau Islands, some 60 km N of the Ujung Kulon Peninsula, but politically part of the same national park. Nearly 30 biologists participated in the expedition (Thornton 1985, Thornton & Rosengren 1987). An auxiliary aim was to examine the biota of selected areas bordering the Sunda Strait to assess likely origins of the Krakatau fauna. Ujung Kulon is one such area. This paper is an appraisal of the butterflies collected and seen there during the expedition.

METHODS

A total of 158 biologist-days was spent in the Ujung Kulon area from 30 August–23 September 1984. Slightly under half of these (73 biologist days) were on Pulau Peucang (Fig. 1), an island of ca. 440 ha separated from the peninsula by ca. 500 m of shallow water. The various sites visited on the W part of Ujung Kulon are shown in Fig. 1. They include a range of representative vegetation types: Pulau Peucang—pes-caprae formations, *Ficus* forest, and various edge habitats; Ujung Kulon—pes-caprae, mangrove, *Radermachera* forest, *Arenga* forest, forest edges, and *Chrysopogon* grassland. Plant nomenclature is based on papers in Flenley and Richards (1982).

Most records are of butterflies collected by the authors, but many other expedition members also contributed specimens. TRN and MBB systematically searched the above-noted vegetation types to observe relative abundance of the species present. Examples of the taxa collected will be deposited in the Museum Zoologicum Bogoriensis, Bogor. Identification was from published literature (including Corbet et al. 1978 and papers referred to therein), and by comparison with collections in Bogor and the British Museum (Natural History), except for Hesperiidae, which were identified by A. F. Atkins. Although Blower and van der Zon (1977) refer to "large entomological collections" from the area, we have not traced any previous lists of butterflies from Ujung Kulon.
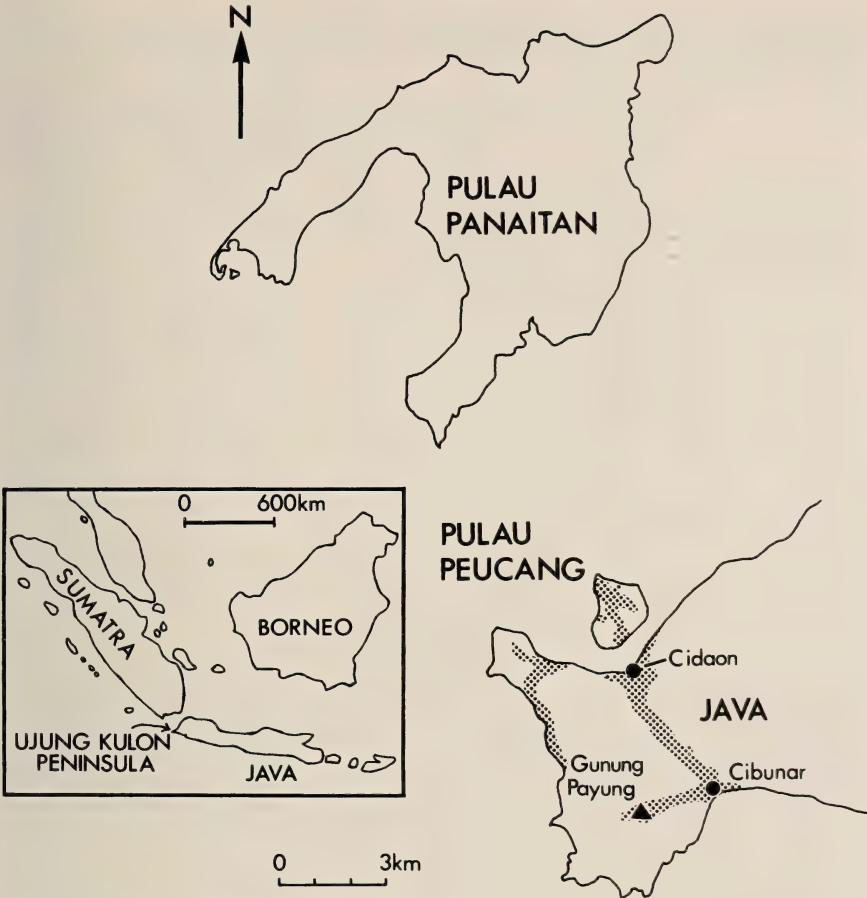
FIG. 1.   Western part of Ujung Kulon peninsula, Java, indicating areas (shaded) where collections were made and locations mentioned in text. Sunda Strait passes between Sumatra and Java, and the Krakatau Islands are in the center of the Strait 60 km N of Ujung Kulon.

RESULTS AND DISCUSSION

Although the butterfly fauna of Indonesia is reasonably well known, at least in gross terms, there are few lists of species in areas of particular biological significance. The fauna of the Krakatau Islands has received much recent attention (Yukawa 1984, Bush 1986, New et al. 1987), and Yukawa (1984) also noted 29 species from Pulau Panaitan, an island of slightly over 12,000 ha separated from Ujung Kulon by ca. 10 km of deep water, and not visited by us. The data presented here thus complement Yukawa's account and, although the species list (Table 1)

TABLE 1. Butterflies recorded in Ujung Kulon Peninsula and Pulau Peucang in 1984 including records in Pulau Panaitan from Yukawa (1984) and incidence of species on the Krakatau Islands.

	Ujung Kulon	Pulau Peu-cang	Pulau Panai-tan	Kraka-taus
Papilionidae				
Pachliopta aristolochiae antiphus (F.)	X			X
P. a. adamas (Zinken)	X	X		X
Atrophaneura coon coon (F.)	X			
Graphium agamemnon agamemnon L.		X	X	X
G. doson evemonides Honrath	X	X	X	
G. macareus macareus (Godart)	X			
Papilio peranthus peranthus F.		X	X	
P. helenus engarius Doherty	X		X	
P. polytes? javanus Felder	X			
P. antiphates Cramer ssp.?	X			
P. memnon anceus Cramer	X	X		X
Pieridae				
Appias indra leptis (Felder)	X		X	
A. lyncida lyncida (Cramer)			X	
A. nero nero (F.)			X	
A. paulina (Cramer)	X		X	
Catopsilia pomona F.	X	X	X	X
Ceporea idith (F.)	X		X	
Eurema blanda (Boisduval)	X	X	X	X
E. hecabe (L.)	X	X		X
Leptosia nina (F.)	X	X		
Gandaca harina harina (Horsfield)	X	X	X	
Pareronia valeria leona (Fruhstorfer)	X		X	
Saletara liberia panda (Godart)	X			
Hebemoia glaucippe (L.)	X			
Danaidae				
Euploea camerelzeman Butler	X			
E. crameri Lucas		X	X	
E. diocletianus F.	X			
E. mulciber mulciber (Cramer)	X	X		
E. m. donada Fruhstorfer	X			
E. modesta Butler			X	
E. leucostictos leucostictos Gmelin	X			
E. tulliolus (F.)		X		
Radena juventa (Cramer)	X	X		X
Tirumala limniace (Cramer)	X			
Nymphalidae				
Agatasa franck Godart	X			
Athyma nefte subrata Moore f. *neftina* (Fruhstorfer)		X		
Cethosia penthesilea methypea (Butler)	X			
C. hypsea Doubleday			X	
C. sp.?		X		
Charaxes sp.			X	
Chersonesia rahria (Moore)	X		X	X
Cirrhochroa tyche (C. & R. Felder)			X	X
Cupha erymanthis lotis (Sulzer)	X	X		
Cyrestis thermire Honrath	X			

TABLE 1. Continued.

	Ujung Kulon	Pulau Peu-cang	Pulau Panai-tan	Kraka-taus
Doleschallia bisaltide pratipa (C. & R. Felder)	X			
Euthalia evelina sikandi (Moore)	X			
E. mahadeva (Moore)			X	
Hypolimnas anomala anomala (Wallace)	X			X
Lebathea martha malayana Fruhstorfer	X			
Lexias dirtea (F.)	X			
Neptis hylas (L.)	X	X	X	X
N. sankara (Kollar)	X			
Pantoporia paraka (Butler)	X			
Phalanta alcippe (Stoll)	X	X		
Precis atlites L.	X	X		X
P. almana javana C. Felder	X			
P. erigone (Cramer)	X			
P. hedonia ida (Cramer)	X			
P. iphita (Cramer)	X			
Tanaecia clathrata (Vollenhoeven)	X			
T. godartii (Gray)	X			
T. iapis (Godart)	X			
T. munda Fruhstorfer	X	X		
Terinos terpander ?*teos* (de Niceville)	X	X		
Satyridae				
Melanitis leda (L.)	X	X		X
M. phedima (Cramer)	X			
Elymnias hypermnestra (L.)	X			X
Lethe confusa Aurivillius	X			
Mycalesis horsfieldi (Moore)	X			X
M. janardana Moore	X			X
Ypthima horsfieldi Moore	X			X
Faunis canens canens Hübner		X		
Lycaenidae				
Liphyra brassolis Westwood	X			
Arhopala antimuta C. & R. Felder	X			
Allotinus horsfieldii Moore	X	X		
A. subviolaceus C. & R. Felder		X		
A. unicolor C. & R. Felder	X			
Catochrysops panormus (C. Felder)			X	X
C. strabo (F.)	X	X		X
Chilades pandava (Horsfield)		X		
Drupadia ravindra Distant	X	X		
Eooxylides tharis distanti Riley	X			
Ionolyce helicon (C. Felder)	X			
Jamides bochus (Stoll)			X	X
J. aratus (Stoll)	X	X		X
J. celeno (Cramer)	X	X		X
J. elpis (Godart)	X			
J. parasaturatus (Fruhstorfer)	X			
J. malaccanus (Röber)			X	
Lampides boeticus (L.)	X	X		X
Miletus ?*boisduvali* Moore	X			X
M. sp.			X	

Table 1.   Continued.

	Ujung Kulon	Pulau Peu-cang	Pulau Panai-tan	Kraka-taus
. *Nacaduba pactolus* (C. Felder)			X	
Neopithecops zalmora (Butler)	X	X		
Pithecops corvus Fruhstorfer	X			
Prosotas nora superdates Fruhstorfer	X			
P. dubiosa (Semper)			X	
Zizina otis (F.)	X	X		X
Zizula hylax (F.)	X			X
Hesperiidae				
Halpe pelethronix Fruhstorfer	X			
Koruthaialos rubecula namata Fruhstorfer	X			
Isma bononia bononia (Hewitson)	X			
I. obscura vulsina Evans	X			
Sancus (*Psolos*) *fuligo fuligo* (Mabille)	X			
Telicota colon vaja Corbet	X			
Zographetus (*Ogygia*) *ogygioides* Elwes & Edwards	X			
Salanoemia tavoyana Evans	X			
Acerbas anthea javanica Snellen		X		
Taractrocera? *aliena aliena* (Plötz)		X		
Potanthus confucius (C. & R. Felder)			X	X

cannot be regarded as comprehensive, it will be of value for comparison with other sites in Indonesia as the fauna is progressively documented.

In Table 1, the species are noted as occurring either on Ujung Kulon proper or on Pulau Peucang. Yukawa's (1984) Pulau Panaitan records are also included, and incidence of species on the Krakatau Islands is indicated.

At least 106 species of butterflies are here recorded from Ujung Kulon and nearby islands; the several noted merely as "sp." are not included in this total because of possible overlap. This figure represents some 18% of the 583 species recorded from Java (Yukawa 1984), and includes representatives of all families except Libytheidae (3 Javanese species) and Riodinidae. The relatively small size of Pulau Peucang rendered our coverage reasonably complete, and the 36 species recorded there are believed to well represent the butterflies then flying on the island.

Vegetation of Ujung Kulon is diverse (Hoogerwerf 1970, Blower & van der Zon 1977, Hommel 1983), and offers a wide range of habitats for butterflies: beach forests with pes-caprae formations, mangrove swamp forests, freshwater swamp forests, and rain forest, and artificially maintained clearings and grasslands.

Distribution of many butterfly species was limited, and clearly related to predominant vegetation types. The pes-caprae formations take their name from *Ipomoea pes-caprae* (L.) R. Br., a common creeper on

accreting tropical beaches growing in association with a mixture of grasses and herbaceous dicotyledons. The pes-caprae formations of both Pulau Peucang and Ujung Kulon were rich in *Jamides* spp., *Catochrysops* spp. and *Eurema* spp. *Catochrysops strabo* (F.) was the commonest of the lycaenids in this association on both Pulau Peucang and Ujung Kulon, a finding which contrasts markedly with its apparent absence from Pulau Panaitan (Yukawa 1984) where its place appears to be filled by *C. panormus* (C. Felder). Both *C. strabo* and *C. panormus* were recorded on the pes-caprae formations on Krakatau, but both were relatively scarce there, and *Jamides celeno* (Cramer) and *J. aratus* (Stoll) were the predominant species. Further work is necessary to establish the seasonality of these species before a significant distribution pattern can be discerned.

The narrow belt of mangroves at Cidaon supported few butterfly species. Those seen flying there, including *Papilio helenus engarius* Doherty and *Melanitis phedima* (Cramer), seldom settled, possibly having strayed from the nearby forest edge.

The forests of Pulau Peucang and Ujung Kulon differ widely in character. Those of the former appear to be more mature, and are dominated by large individuals of *Ficus pubinervis* Bl. and strangler figs, which form a canopy at ca. 30–35 m. The canopy produced by these species is dense; little light reaches the forest floor, and there is very little undergrowth between the widely spaced trunks. Only *Terinos terpander* ?*teos* (de Niceville) and *Melanitis leda* (L.) were recorded within this forest. However, where trees had fallen, creating an opening in the canopy, *Phalanta alcippe* (Stoll) and *Drupadia ravindra* Distant were present. This forest is in some ways comparable to the *Ficus pubinervis* forest of Rakata, Krakatau. On Rakata the *F. pubinervis* forest is not so well established, and there is a dense undergrowth of pteridophytes and *Smilax zeylanica* L. The last is a forest creeper which has been suggested as the foodplant of the only deep-forest butterfly on Krakatau, *Loxura atymnus fuconius* (Stoll) (Bush 1986). Notably, neither *L. atymnus* nor *S. zeylanica* were recorded during our visit to Pulau Peucang.

One similarity between the forests of Krakatau and Pulau Peucang is the lack of impact of footpaths. On the latter, the trunks of trees are so widely spaced that there has been no need to fell trees to create paths, and thus the canopy remains unbroken. Krakatau has no footpaths; the only clearings are where trees have fallen. This contrasts with Ujung Kulon where the denser forest growth necessitated limited clearing for footpaths. The result is the creation of forest "rides", where more light reaches the forest floor. If the butterflies found along these forest paths are used as an indication of the overall species composition

in forest areas, two points must be borne in mind. First, there is an increased butterfly population taking advantage of the flush of herbaceous growth along the footpath, and this might give a misleading impression of the density of butterfly populations. Second, there is the problem of dissociating those species which are true deep-forest butterflies (and have been found by chance along the ride) from those species which are woodland-edge species and would not be found there but for the increased light availability. An impression of butterfly numbers and species diversity in the true forest can only be obtained away from the paths.

Butterflies which seemed to be characteristic of the Ujung Kulon forest interior were *Pithecops corvus* Fruhstorfer, *Arhopala antimuta* C. & R. Felder, *Agatasa franck* Godart (the last seen roosting high on tree trunks), and locally *Lexias dirtea* (F.) (found only on the higher slopes of Gunung Payung (480 m)).

The forest edge habitat on Pulau Peucang was probably oversampled compared with other areas, as the clearing surrounding the park office bungalows where we were based was the nearest and easiest area to collect in. Pink and red-flowering garden shrubs attracted a variety of danaids including *Euploea crameri* Lucas, *E. mulciber mulciber* (Cramer) and *Radena juventa* (Cramer). Another common visitor to these shrubs was *Papilio peranthus peranthus* F., although it appeared to be scarce in the rest of the reserve, and was not recorded at all from Ujung Kulon. *Graphium agamemnon* L., *Precis atlites* L. and *Neptis hylas* (L.) were among other heliophilous species recorded in the clearing.

Forest-edge areas on Ujung Kulon are a varied set of habitats determined by the surrounding forest type. There is additional habitat diversity created by stream banks. Many species were collected along forest paths, or in clearings where trees had fallen. Some of those that may be true forest species were *Leptosia nina* (F.), *Allotinus* spp., *Lebathea martha malayana* Fruhstorfer (?), and members of the *Euthalia-Tanaecia* complex. Species that seemed more light-demanding recorded along paths were *Hebemoia glaucippe* (L.), *Appias* spp., *Atrophaneura coon coon* (F.) and *Ypthima* spp. Many Pieridae were captured on flowers or at streamsides; the most abundant were *Eurema* spp. and *Catopsilia pomona* F., the latter migrating at the time of our visit (New et al. 1985). The various species of *Appias* were all taken in open glades or at the edge of the forest where, like *H. glaucippe*, they visited flowering shrubs. Although some of the pierids were caught near streams, there were no marked concentrations of butterflies on stream banks.

In Ujung Kulon the extensive *Chrysopogon* grassland communities maintained for herds of banteng, *Bos javanicus* (d'Alton), did not ap-

TABLE 2.   Numbers of butterfly species shared between areas of western Java and the Krakatau Islands.

	Ujung Kulon	Pulau Peucang	Pulau Panaitan	Krakatau Islands
Ujung Kulon	—	24	11	22
P. Peucang	—	—	8	15
P. Panaitan	—	—	—	9
Total	85	36	29	54

pear to support a rich butterfly fauna. This, however, may have been due to cloudy conditions when collecting was carried out on the main grassland area at Cidaon. The abandoned field systems around Cibunar were rich in flowering herbs such as *Eupatorium odoratum* L., which attracted *Neptis* spp. and *Pachliopta aristolochiae* (F.).

The eight species of Hesperiidae recorded from Ujung Kulon were captured along forest tracks or at the forest margin. None was taken on the grassland expanses of Cidaon or Cibunar. These are all woodland or semi-woodland species. The eight species of Hesperiidae from Krakatau were caught in grassland or beach habitats, and habitat preferences may thus account for the lack of overlap of species between the two localities.

One butterfly recorded regularly on Krakatau (and also at Carita, W. Java) was *Troides helena* (L.). However, neither *T. helena* nor the closely related *T. cuneifer* (Oberthür) were recorded from Ujung Kulon or associated islands. *Delias* spp., which might have been expected in the forests at Ujung Kulon, were notably absent. This genus was also absent from Krakatau, but there the reason is likely to be the absence of the foodplants (Loranthaceae).

Degrees of overlap of species found on Ujung Kulon, Pulau Peucang, Pulau Panaitan, and the Krakatau Islands are shown in Table 2. Many of the 54 species found in recent collections from Krakatau (New et al. 1987) were not found in the Ujung Kulon area.

Tables 1 and 2 should be interpreted with caution as the survey of Ujung Kulon was far from complete, and the low values obtained from Pulau Panaitan suggests that it, too, may have been undersampled. It is likely that all the species found on Pulau Peucang and Pulau Panaitan are present on Ujung Kulon even though they were not recorded during this census. From the data available, the degrees of species overlap of Ujung Kulon with Pulau Peucang and Krakatau are almost equal. However, the species are not the same in each case. Fourteen species have been recorded as common to all three localities. These species are either highly mobile-migratory or inhabit the coastal vegetation and pescaprae associations. *Radena juventa*, *Neptis hylas* and *Catopsilia po-*

mona which are geographically widespread or migratory, tend to be polyphagous, and are, therefore, likely to be successful colonizers. Species that may be more specific in their foodplant requirements, including the species of the pes-caprae formations, must rely on their habitat being present at a new site if colonization is to be successful. In coastal species, two factors aid dispersal to islands. First, they are likely to be blown out to sea, and second, the plants adapted to beach environments are likely to be among the first colonizers of an island where plant recolonization is taking place. Thus the foodplants are available for the coastal butterfly species on their arrival. Woodland butterfly species may have to arrive many times before they find a suitable habitat. This might help to explain the apparent paucity of woodland butterfly fauna on the offshore islands considered in this paper compared to the diverse species list for forest edges and coastal environments.

Particular families also overlap. As already noted, there was no overlap between the Hesperiidae of the Krakatau Islands and those of Ujung Kulon, and yet five out of eight species of satyrids found on Ujung Kulon were also found on Krakatau. In all the areas visited the commonest member of the Satyridae was *Melanitis leda*.

Many Lycaenidae were captured in small numbers, and because of the existence of species complexes, exact identification is not always clear. A single specimen of *Liphyra brassolis* Westwood is of interest, as this species is apparently rare in much of Indo-Malaya (Corbet et al. 1978). Miletinae were represented by species of *Allotinus* and *Miletus*, and Polyommatinae were by far the most diverse group of lycaenids present. The species shared with the Krakatau Islands are predominantly those associated with lowland Leguminosae, including the pes-caprae coastal vegetation which is also an important butterfly habitat on the Krakatau Islands (Bush 1986, New et al. 1987). Theclinae were relatively scarce, although one species of the complex genus *Arhopala* was found; the single species of *Eooxylides* and *Drupadia* are both widely distributed in Sundaland, but have not been found on Krakatau.

Hesperiidae can be identified only with some reservations. Only females of *Taractrocera a.* ?*aliena* (Plötz) were taken, for example, and male genitalia are necessary for confirmation of species identification. Most of the species records are based on single individuals.

CONCLUSIONS

All the butterfly species captured are likely to be resident in the area, and the vegetational diversity is clearly sufficient to support an enormous spectrum of Lepidoptera. The range from mature forest to cleared ground provides a diversity of successional stages. The present conser-

vation policy of maintaining cleared areas for grazing by banteng helps to foster such diversity. It has been suggested that there should be a management policy to create forest glades to provide improved grazing for the Javan rhinoceros. Such areas would also help to maintain butterfly diversity, but felling would have to be done with sensitivity to leave areas of mature forest for species that are dependent on deep-forest habitat. However, as Hommel (1983) suggests, clearings are produced naturally when giant forest trees fall. This natural process, combined with maintenance of the footpath system, could provide habitats similar to those advocated by Schenkel et al. (1978) without recourse to more active management. Further study is needed to determine the distribution of particular butterfly species on Ujung Kulon, but this brief survey, although restricted to the western region of the park, indicates that some species may be both rare and localized. Butterfly diversity in this area may well depend on the maintenance of the greatest possible range of vegetation types.

ACKNOWLEDGMENTS

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THE IDENTITY OF *CYCLOPIDES PAOLA* PLÖTZ (HESPERIIDAE)

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ABSTRACT. *Cyclopides paola* Plötz, described from Angola, is placed in the combination *Kedestes nerva paola* (Plötz), new status. *Kedestes protensa* Butler, previously regarded as a subspecies or synonym of *K. paola*, is reinstated as a species. Records of *K. nerva* (Fabricius) from Zimbabwe and Kenya are rejected.

Additional key words: Africa, taxonomy, *Kedestes protensa, K. nerva.*

Ever since Plötz (1884) described *Cyclopides paola* from Angola, its identity has been a source of confusion. Its generic placement was questioned by Holland (1896), while Swinhoe (1908) referred it to *Kedestes* Watson, and published a color figure based on Plötz's original unpublished illustration, noting that it could belong to either *K. nerva* (Fabricius) (=*tucusa* (Trimen)) or *K. protensa* Butler. Evans (1937) regarded it as conspecific with *K. protensa*, with the latter a subspecies. The presence of a complete marginal line on the underside of the hindwing in the figure of *paola*, plus Evans' association of the taxon with *K. protensa*, led Hancock and Gardiner (1982) to synonymize the two, since Evans' (1937) interpretation of *paola* as a subspecies was at variance with available material. As used by Pennington (1978), the name *paola* is now known to refer to three separate species: *K. protensa, K. michaeli* Gardiner & Hancock and *K. monostichus* Hancock & Gardiner (Hancock & Gardiner 1982).

The capture in NW Zambia of a fresh pair of *K. nerva* (Ikelenge, 5 May 1983, D. Heath; in A. Heath Collection, Cape Town), and a re-examination of the male from Mwinilunga recorded and illustrated in Hancock and Gardiner (1982) (in Natural History Museum of Zimbabwe, Bulawayo), revealed minor differences in wing pattern between them and typical examples of *nerva* from South Africa, although there are no discernible differences in male genitalia. These Zambian males of *K. nerva* agree more closely with the figure of *paola* given by Swinhoe (1908) than do specimens of *K. protensa* from the same area (figured by Hancock & Gardiner 1982 as *paola*), particularly with regard to the elongate white spot in space 2, the pale area beyond the cell on the forewing underside, and the ground color and distribution of the black spots on the hindwing underside. In size too, the Zambian *nerva* agree with the type of *paola*, while *protensa* is a distinctly larger species. The marginal line on the hindwing underside is a series of streaks, interrupted at the veins, and not a continuous line as shown in Swinhoe's (1908) figure.

The original description of *paola* by Plötz (1884) is sketchy, and the

marginal line on the hindwing is not mentioned. The type is apparently lost, and subsequent interpretations of the species appear to be based on Plötz's unpublished plate (the present whereabouts of which, if still extant, is unknown to me), and on the reproductions by Swinhoe (1908) and Aurivillius (1925). The continuous marginal line on the hindwing, evident in figures of the latter two authors, is apparently an error. It may well be present also on the original figure, as the line appears continuous unless examined closely; the streaks are longer and not as distinct as in typical examples of *K. nerva*.

Kedestes protensa (=*K. paola* of Hancock & Gardiner 1982) and *K. nerva* differ in wing size and in shape of male genitalia, particularly the serrate apical area of the harpe, which is narrower and projecting in *K. nerva*. In pattern, apart from the hindwing marginal line, the two species differ in the arrangement of the black spots in the postdiscal band on the hindwing underside; the inner row of spots is distinctly W-shaped in *K. nerva*, V-shaped in *K. protensa*. The taxon *paola* differs from both these species in the reduced pale spot in space 1b of the forewing, but it agrees with *K. nerva* in male genitalia and other pattern characters. The ground color of the hindwing underside is browner in *paola* than in the other species, but this color is approached in some examples of *nerva* from South Africa, although an orange tint is usually evident. Accordingly, *K. paola* is placed here as a subspecies of *K. nerva*. Illustrations of these taxa may be found in Hancock and Gardiner (1982) and Pennington (1978), but in both cases Zambian examples of *K. protensa* are misidentified as *K. paola*. Hancock and Gardiner (1982) also figured male genitalia.

The establishment of the true identity of *K. paola* necessitates an adjustment to the nomenclature of *K. nerva* and *K. protensa* from that given in Hancock and Gardiner (1982). *Kedestes paola* is separable as a subspecies of *K. nerva* on pattern characters. The revised nomenclature is presented below.

Kedestes nerva nerva (Fabricius)

Hesperia nerva Fabricius, 1793:340. Type from "Indiis", locality error, *recte* Natal, South Africa.
Pyrgus tucusa Trimen, 1883:359. Type ♀ from Natal, South Africa.

This subspecies appears to be restricted to South Africa, being recorded from the provinces of Natal and Transvaal. Records of Zambia (Hancock & Gardiner 1982) belong to the following subspecies, while those from Zimbabwe (Pinhey 1949, Pennington 1978) and possibly Kenya (Evans 1946) appear to belong to *K. michaeli*. Examination of a female of *K. michaeli* from Zimbabwe (Bromley, 23 August 1967, E. O. Martyn; in Natural History Museum of Zimbabwe, Bulawayo), iden-

tified by the collector as *K. nerva,* illustrates the confusion that existed between these two species, making the untraced Salisbury record of *K. nerva* noted by Hancock and Gardiner (1982) very unlikely. Evans (1946) noted that the Kenyan specimens he examined were not quite typical of *nerva,* and these and the Zimbabwe records are therefore rejected.

Kedestes nerva paola (Plötz), new status

Cyclopides paola Plötz, 1884:392. Type ♂ from Angola.

This subspecies is known from Angola and the Mwinilunga district of NW Zambia. It differs from typical *nerva* in the reduced white spot in space 1b on the forewing, and in the browner ground color and better developed marginal streaks on the hindwing underside. Evans (1937) appears to have confused this taxon with *K. michaeli,* and all his records from Zambia, Zaire, and Angola probably belong to this latter species, suggested by the presence of only a single cell spot on the forewing. This cell spot is divided into two in *nerva* and *protensa.*

Kedestes protensa Butler, revised status

Kedestes protensa Butler, 1901:59. Type ♂ from N. Nigeria.
Kedestes chacoides Gaede, 1915:126. Type ♂ from Busantare, Cameroon.
Kedestes paola protensa Butler; Evans, 1937:84.
Kedestes paola; Pennington, 1978:fig. 724 ii; Hancock & Gardiner, 1982:120. Misidentifications.

This species is known from Sierra Leone, Nigeria, Cameroon, Uganda, S Sudan, and NW Zambia. It appears to prefer swampy areas of grassland, a moister habitat than that apparently preferred by *K. nerva.*

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MATE LOCATION BEHAVIOR OF THE LARGE SKIPPER BUTTERFLY *OCHLODES VENATA*: FLEXIBLE STRATEGIES AND SPATIAL COMPONENTS

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ABSTRACT. Male *Ochlodes venata* were studied in lightly wooded heathland at Lindow, Cheshire, U.K., using a combination of transects and more detailed observations of movements and behavior in a woodland clearing. Males locate mates by perching and patrolling but are also opportunists and approach females when feeding. Behavior is flexible, and varies with time of day, weather, season, and location. On clear, sunny days, males show a significant bias for patrolling during mid- and late morning, and for perching during early morning and afternoon. Switches then from one activity to another are not entirely related to temperature and energy levels, and may depend on availability of females, males perching when females are relatively scarce. Scent seems to play a prominent part in the location of females during patrolling. Defended territories are located at topographic vantage points (at habitat edges and path junctions), and have a biased distribution to areas where female resources (nectar, oviposition sites) are also available. Territories and even the same perches (specific locations where the insects alight) within them are used by different individuals in the same and different years.

Additional key words: Hesperiidae, England, territoriality.

In the process of obtaining mates, male butterflies are described by Scott (1974) as adopting one of three strategies: perching or waiting for them, patrolling or actively seeking them in flight, and locating them with the use of long-distance pheromones. The last is regarded as of rare occurrence and understood to be a proximate cue (Scott 1972), vision dominating long-distance communication. But *Heliconius erato* males locate preemergent females using chemicals emitted by the pupae (Bellinger 1954). Perching males select characteristic sites, distinct in surface, height, and situation where they bask in the sun and launch themselves at passing insects (Baker 1972, Davies 1978, Dennis 1982a, Bitzer & Shaw 1979, 1983). Patrolling males typically cover much larger areas but differ in the extent and nature of the areas covered (Courtney 1980, Dennis 1982b, Peachey 1980). Scott (1974) regards these processes as distinct; when perching occurs the females necessarily find males, but patrolling males actively find females. Perching has been likened to territoriality by Baker (1972), since defense of some "resource" is involved, but this is denied by Scott (1974).

Recently, mate location behavior has been shown to be more varied. Perching and patrolling provide alternative strategies in some species depending on demographic trends (distribution of females, male-female

ratio) and environmental conditions (sunshine and temperatures, time of day, habitat topography, physical resources) (Scott 1975, 1983, Dennis 1982a, Shreeve 1984, Rutowski 1983, Wickman 1985a). Moreover, it seems that many butterflies adopt intermediate strategies, involving intermittent flight, basking, and feeding bound only to loose areas and without territories, where males are constantly vigilant for females (Dennis 1982a, Morton 1985).

The various aspects of mate location in butterflies are far from resolved. The present paper on *Ochlodes venata* (Bremer & Grey) responds to the need for comparative data. In particular, it addresses issues of territoriality, switches in mate location activity, and siting and structure of territories. *O. venata* is single-brooded in Britain and flies from the latter half of June into late July (Heath et al. 1984).

METHODS

The study was conducted intermittently over a three-year period (1983 to 1985) at Lindow Common near Wilmslow in Cheshire, U.K. (grid reference SJ834812), a 16-ha site of special scientific interest, comprising patches of dry heath (*Calluna vulgaris* with *Ulex* spp., *Vaccinium myrtillus*, and *Deschampsia flexuosa* over podsol soils on fluvioglacial sands) and wet heath (*Calluna* and *Erica tetralix* on permanently wet peaty soils over boulder clay), encircled by *Betula-Quercus* woodland. The site is intensively used for recreation and is crisscrossed by paths and tracks.

Data were obtained by recording behavior and location of adults along repeated transects over fixed routes (Pollard 1977, 1979). Transects were established at two scales, one covering the variety of vegetation zones on the common, the second limited to a small clearing. The clearing was divided down the center into two zones, and observations made from the wooded margin. Transects were walked at a standard pace 6 times over 20 min in each hour. The clearing comprises an open space some 25 m by 18 m divided into 2 zones of *Molinia caerulea* and *Calluna,* and surrounded by birch canopy and furze. Spatial data were plotted on an Ordnance Survey 1:2,500 base and on a detailed plan of the clearing (Fig. 1). More intensive observations were made using a cassette recorder relating behavior and movements of adults to coded landmarks. Individuals were followed as long as possible (minimum of 3 min), and activities divided into the following categories: resting, basking, feeding, flight, interspecific interaction, conspecific interaction, attempted courtship, and inspection. To these were added locational data and as much interpretation as feasible. Capture of individuals for marking was found to affect their behavior, and for these observations each male required a unique mark. The
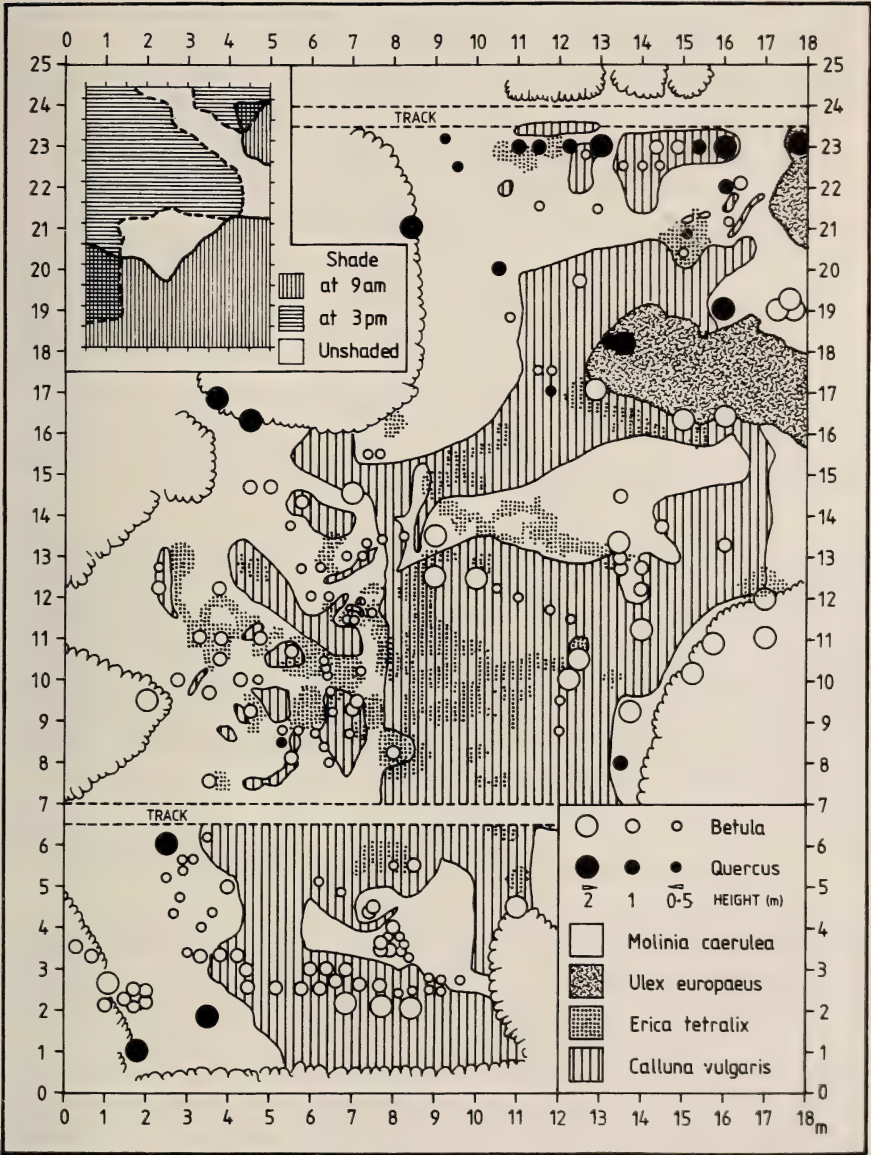
FIG. 1. Topography, vegetation, and shading of the clearing used for observations on territoriality. The scale around the edge of the map is also used as a coordinate system for Figs. 5, 6, 7 and 8.

TABLE 1.   Counts of male *O. venata* for different habitats and associated flora from 9 transects on Lindow Common.

	F	% I	% T
Habitat			
Woodland cover	0	0	26
Woodland glades & fringe	132	68	42
Open sward	43	22	27
Open track	20	10	5
Woodland bramble	0	0	5
Associated flora for open areas			
Calluna	7	4	30
Molinia	156	96	70
Tall-herb grassland	11	5	9
Bramble	97	50	13
Dry heath	10	5	19
Wet heath	11	6	9

F, number of adults; % I, percent of insects recorded on transects; % T, percent of transect associated with the habitat and flora. Based on 195 insects. Length of transect 2.24 km.

marking of individuals varied sufficiently for them to be traced following interactions with other males. Observations on particular individuals ceased if there was doubt as to their identity. All cassette recordings and transect observations were carried out in cloud-free conditions with shade temperatures above 20°C. As part of the program to determine the factors in the selection of perch sites, an artificial landmark (a white plastic bag) was used in the clearing, alternated with the natural background for identical observation periods.

RESULTS

Distribution of Adults on Lindow Common

Males have a clustered distribution on the common. They are not found under woodland shade (Table 1, $\chi^2_{(1)} = 69.1$, P < 0.001) and, in open areas, show a bias for wet heath, *Molinia* grassland, and tall-herb grassland as opposed to *Calluna* and dry heath (Table 1, $\chi^2_{(1)} = 35.5$, P < 0.001). There is no preference for clearings and open spaces surrounded by woodland compared to open areas extending beyond woodland ($\chi^2_{(1)} = 1.78$, P > 0.1). Edge sites are preferred, along tracks in the woodland or out on the open heath, at path junctions, in woodland clearings, and along the woodland fringe, males congregating at boundaries between tall and short vegetation rather than in open expanses of low growth (comparison with bramble areas excluded, $\chi^2_{(1)} = 35.1$, P < 0.001). However, males significantly "clump" on bramble bushes (*Rubus* spp.) most of which are also located by the side of tracks or at path junctions ($\chi^2_{(1)} = 223$, P < 0.0001), but ignore bramble under dense woodland cover ($\chi^2_{(1)} = 47.7$, P < 0.001).
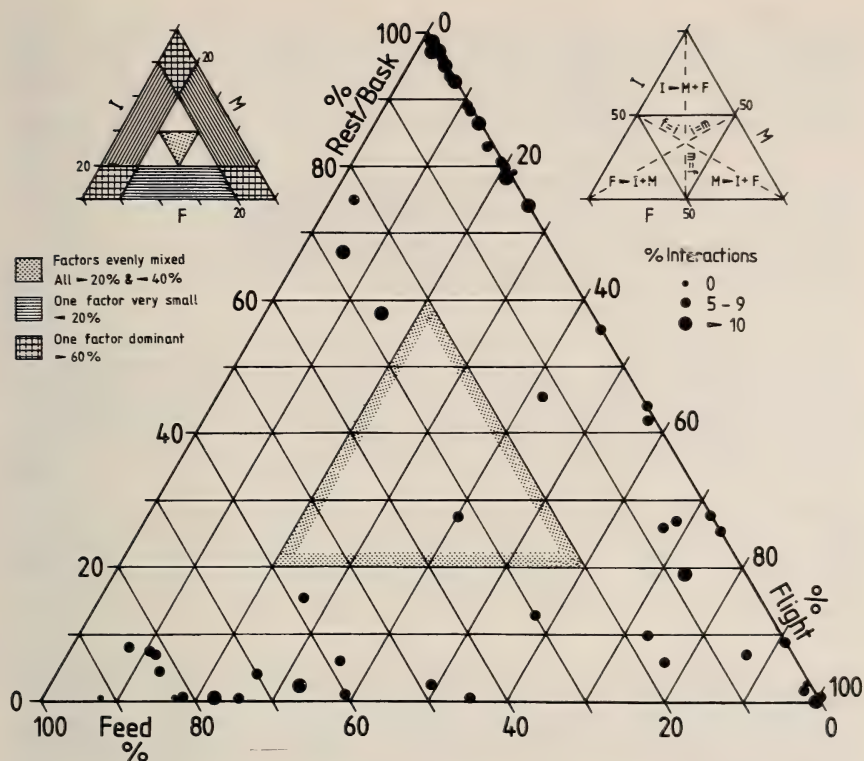
FIG. 2. Behavior of 54 male *O. venata* observed for at least 3 min each (mean time = 405 sec, standard deviation 249 sec) recorded in triangular co-ordinates for basking, flight and feeding. Percentage interactions are overlaid as proportional symbols. Inset diagrams: I, inactive; M, mobile; F, feeding.

The female distribution is very similar to that of the males. On Lindow, *O. venata* larvae feed mostly on *Molinia*; females regularly oviposit on this grass and have been reared on it (Bink 1985).

Modes of Behavior

Modes or patterns of behavior are made up of individual acts of behavior. This is evident from placing 54 males in triangular coordinates for flight, basking-resting, and feeding. Several distinctive features emerge (Fig. 2). With three exceptions, males are restricted to areas on the graph where one activity is virtually dominant. Males do not behave randomly but bask, fly, or feed for extended periods, although grades of activity occur between flight and feeding and between basking and flight (far less between feeding and basking). Conspecific interactions (skirmishing between males and attempted courtship) occur for

each of these activities, which suggests that the butterfly is opportunistic in mate location. However, interactions are more frequent when males are basking. We argue that three distinctive types of behavior exist in male *O. venata*: perching, patrolling, and feeding. These behaviors are perhaps better visualized in the form of real-time plots of activity (Fig. 3), and become easy to distinguish using the spatial components of each behavior pattern, as will become clear below.

The perch behavior (Fig. 3a) is restricted to small areas, where a vantage point is adopted. Here, male *O. venata* bask in the sun and "sortie" after passing objects. Response to the latter varies dramatically from rapid inspections to violent spirals and chases depending on (i) the insect involved, (ii) the sex of the intruder if conspecific and (iii) prior ownership of the area. Conspecifics induce much greater activity than nonconspecifics, and contested ownership of the space leads to the most violent aerial activity, during which the impact of the males can be heard. Interactions between male *O. venata* are significantly longer when one of the males is territorial than when both are feeding or patrolling ($t = 3.98$, P < 0.001) (Table 2) (compare Wickman & Wiklund 1983, Wickman 1985b). Passing females trigger attempted courtship, though males are usually easily put off by fecund females, which flutter their wings and, having landed, on occasion, raise their abdomens. We suggest that some chemical deterrent is released. Males repeatedly return to perches in the same small area, which distinguishes this activity from patrolling. Perches are typically low vegetation, small seedlings of oak or birch, bramble leaves, occasionally herbs or grass stems, which barely overtop the ground vegetation. Only rarely are perches more than 1 m above the ground adopted, but the butterfly will rest (become inactive) on vegetation above this level. Males feed least during perching; apart from interactions, flight is restricted to short investigative patrols (as distinct from continuous patrolling) within and immediately beyond the area occupied.

At perch sites, extended interactions occur that are not simply the result of the resident male investigating the sex of the intruder and the intruder attempting to escape from a would-be predator (Scott 1974). Not only is female response to male approaches very different (many land and engage in mate-refusal posture), but this would not explain why intruding males (recognizable from wing marks) return after what can only be described as extremely violent aerial combat, and why such sorties take place back and forth over the area involved. The relation between the aggression of the incumbent and the inclination of the intruder to leave attests further the defensive role of interactions. Specific tolerance thresholds need to be exceeded before intruders leave an area, and similarly determine whether incumbents stay or abandon
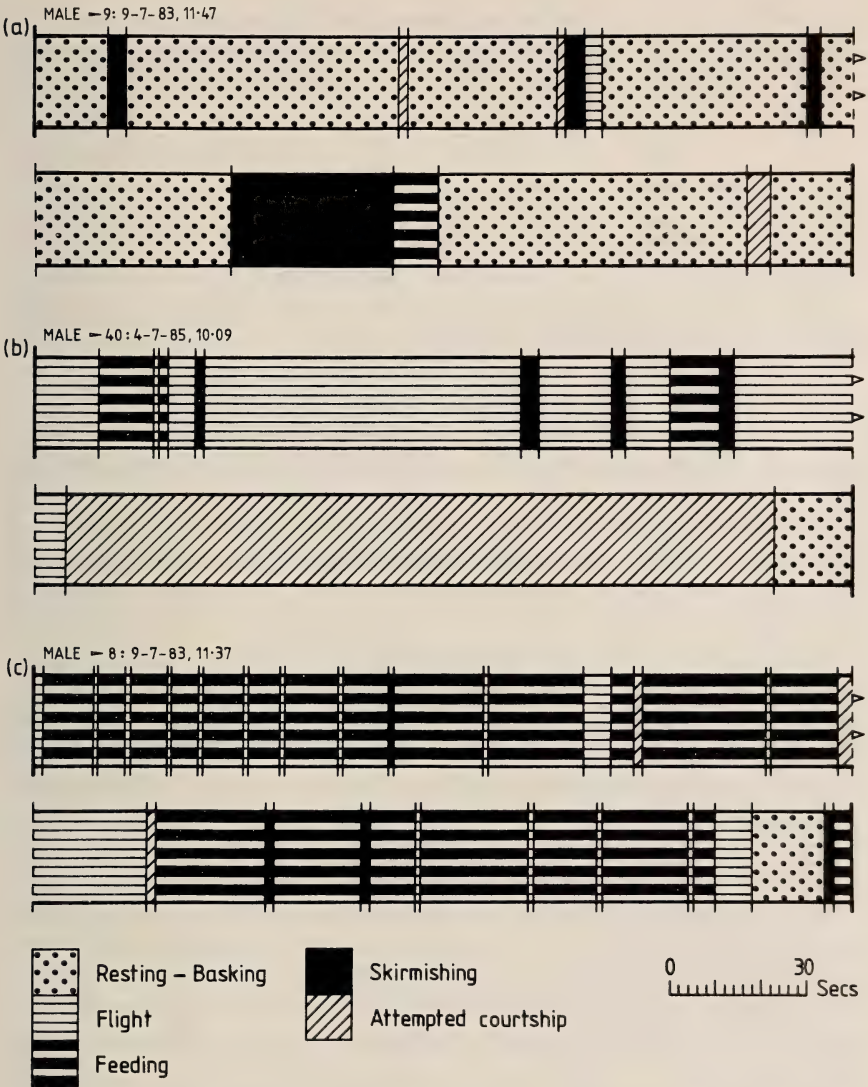
FIG. 3.   Real-time plots of changing behavior in three male *O. venata* engaged in (a) territorial activity, #9, 1147 h, 9 July 83, (b) patrolling, #40, 1009 h, 4 July 85, (c) feeding, #8, 1137 h, 9 July 83.

territories. To some extent it was possible to simulate these responses using a net. Perching males that are merely disturbed by passing a closed net over them invariably return to the perch; those caught in the net bag and released in one gentle move usually return or retire to an area nearby, and return within 10 seconds. Males caught in a sweep

TABLE 2.   Duration of interactions between male *O. venata* and other insects.

Interaction	Statistics[a]	Perching	Patrolling and feeding
Between males	$\bar{x}$	7.7	4.3
	SE	0.7	0.4
	n	73	28
With other insects[b]	$\bar{x}$	2.4	2.5
	SE	0.1	0.3
	n	76	16
Attempted courtship	$\bar{x}$	3.8	3.8
	SE	0.7	0.3
	n	12	43

[a] $\bar{x}$, mean time (seconds); SE, standard error; n, sample size.
[b] Other insects include *Maniola jurtina*, bees, and flies (mostly syrphids).

of the net and then released exit in a straight line at high speed never to return (Fisher exact test, P < 0.001) (Table 3). This not only has connotations for territoriality but also for mark, release, and recapture work with *O. venata*. Finally, *O. venata* males reveal distinct signs of pugnacity to other insects, such as syrphids, which hover in the area, effecting direct onslaughts rather than gentle investigative flights of which they are capable.

Patrolling (Fig. 3b) is distinguished by extended and spatially unbounded flights. The flight can be very slow, at any height up to 3 m, but is usually very low, where the butterfly engages in weaving, scanning, hovering, often circular inspections interspersed with infrequent halts (physical inspections), but always remaining close to vegetation, skimming over its surface. Flight can also be much faster, several m/second, apparently when the butterfly is changing location, and cues are weak. Patrolling behavior is intensive and seems to be influenced strongly by scent. One male was observed searching a 1 m tall birch seedling systematically for 15 min, weaving in and out of the twigs and leaves, before it found the female. The female left the clearing followed by the male. On other occasions, persistent searches by males of small areas (<0.5 m²) in circuits were witnessed where females were found eclosing.

Males feed while patrolling, but for short sessions. They also bask and rest, especially after extensive flight, although platforms differ from territorial perches (occurring at a greater range of heights up to 3 m; territorial perches are below 1 m), and are used once only. Skirmishes with conspecifics take place; some of these may well be short inspections, but many are sharp interactions which effect spacing of individuals.

Feeding behavior (Fig. 3c) is equally distinctive, involving short feeding sessions interspersed by "hops" or short flights from flower to flower. Short periods of basking and resting occur as do longer flights

TABLE 3. Effect of artificial disturbance on territorial male *O. venata*.

Disturbance level	:	Direct return	Delayed return	Rapid, linear exit
Closed net swept above insect		10	0	0
Gentle capture		6	3	2
Determined capture		0	0	7

as the butterfly relocates to new resources. Mate location is opportunistic rather than directly sought, non-conspecifics being ignored, and skirmishes with conspecifics being brief but pugnacious or investigative. Attempted courtships also occur frequently, males tending to harrass nonreceptive females feeding on the same resource. The length of each feeding episode depends much on the nectar source, and is longer on *Rubus* spp. and *Hierarchium* than on *Erica tetralix*.

The above three modes of behavior are distinctive and facilitate the classification of the 54 individuals in the ternary graph. Even so, only occasionally was it possible to follow males long enough to note switches from one behavior to another, although a number of males were seen to abandon territories, usually after prolonged periods of inactivity when intruders were lacking.

Switches in Mate Location Activity

Typically, males patrolled in the morning and perched in the afternoon (transect data over heath: $\chi^2_{(1)} = 5.8$, P $<$ 0.02; observations in clearings: $\chi^2_{(1)} = 33.8$, P $<$ 0.001). The number of males engaging in territoriality increased in the afternoon in areas lacking nectar ($\chi^2_{(1)} = 13$, P $<$ 0.001) and in areas having it ($\chi^2_{(1)} = 4.8$, P $<$ 0.05). This pattern was influenced by weather. During cloud-free days (Fig. 4), males perch early but switch to patrolling after 1000 h. In the afternoon, there is a reversion to perching, and some new territories are established. However, in favorable locations, territorial males can be found throughout the day, as in the clearing (Fig. 1). Similarly, patrolling males can be found in the afternoon, but there is typically a great reduction in patrollers in the wet heath areas during afternoon. This pattern was much affected by weather; after overcast mornings, males patrolled in the afternoons. The marked diurnal pattern may also break down during the season. Preliminary observations point to a bias towards perching at the outset of the flight season and at the very end when unmated females are scarce. On 23 July, an equal number of perching males were recorded in the morning and afternoon. Other factors can lead to a breakdown of the typical model. During 1985, emergence was delayed by cloudy and cool weather during the last week of June. When conditions changed on 1 July, an abundance of fresh males and females
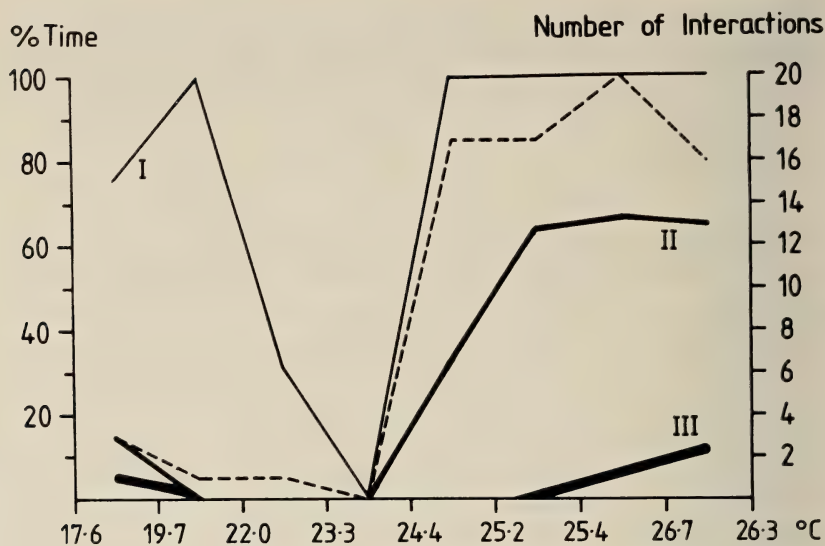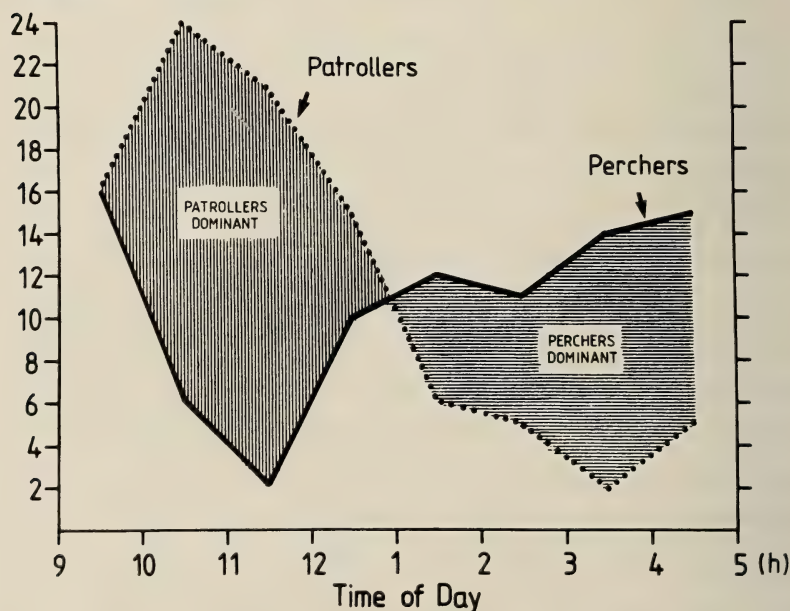
FIG. 4. Diurnal changes in male *O. venata* behavior in the clearing for clear sky conditions on 7 July 1984. Top: Percentages of territorial males and number of interactions between conspecific males (for 20 min in each h) in the main territory centering on map coordinates 070100. Intermittent line, number of interactions. Number of males in territory: line I, 1; line II, 2; line III, 3. Bottom: Frequency of territorial males and patrollers

appeared, and males patrolled as much in the afternoon as in the morning (perch:patrol, 1:2.75 to 1:2; $\chi^2_{(1)} = 0$).

Territories

Location of territories. Transect data over the common revealed that males establish territories at edge or junction sites mainly at woodland margins. Sites without nectar are less favorable as males establish territories in these areas only in the afternoon. A comparison of two groups each comprising four woodland margins equal in size and similar in aspect differed in the number of territories they contained on the basis of a nectar source, bramble ($\chi^2_{(1)} = 6.72$, P < 0.01).

Repeated transects (6/h) in the clearing throughout the day for several days revealed that territories were established in two main areas (Fig. 5): in the middle of the clearing (map grid reference 070100) and in the NW part of the site (map grid reference 1222). The canopy edge facing direct sunlight, the tall birch seedlings in the center of the clearing and the main body of heather and furze were all generally ignored. Crowding of the clearing by males led to a number of subsidiary territories being established in the afternoon, but the main territories occupied edge sites, exposed to sunshine, between the hostplant and some other vegetation type. The central territory was not affected by shade at any time of the day and included an extensive area of *E. tetralix*, a major nectar source. By comparison, the NW territory was abandoned in the late afternoon when it became shaded and nectar sources were limited.

Except for the central territory, the pattern of perches was noticeably affected by the diurnal changes in shade, a significant shift in territories occurring from W to E as the day progressed ($\chi^2_{(1)} = 16.38$, P < 0.001). None of the perch sites below vertical coordinate 07 was occupied before 1200 h. Apart from this diurnal shift, the pattern of territories remained virtually stable from year to year. There is, however, clear indication of a seasonal shift in perches in the central territory, a significant movement northwards in perches between 3 and 7 July 1984 ($\chi^2_{(1)} = 7.41$, P < 0.01) and between 7 and 23 July 1984 ($\chi^2_{(1)} = 6.38$, P < 0.02). This coincided with a shift in flowering of *E. tetralix*, from the shorter *Molinia* zone to the *Calluna* sward where it is partially overtopped. Males were perching 10 cm higher on 23 July and therefore in a cooler microclimate during cooler conditions (maximum temperatures: 7 July, 27°C; 23 July, 24°C; windspeed: 7 July, 3.4 knots; 23 July, 5.9 knots).

←
from 48 transects covering clearing. Mean hourly number is obtained by dividing numbers in activity by 6. The few males feeding have been omitted. Shade temperatures are given for each hour (°C).
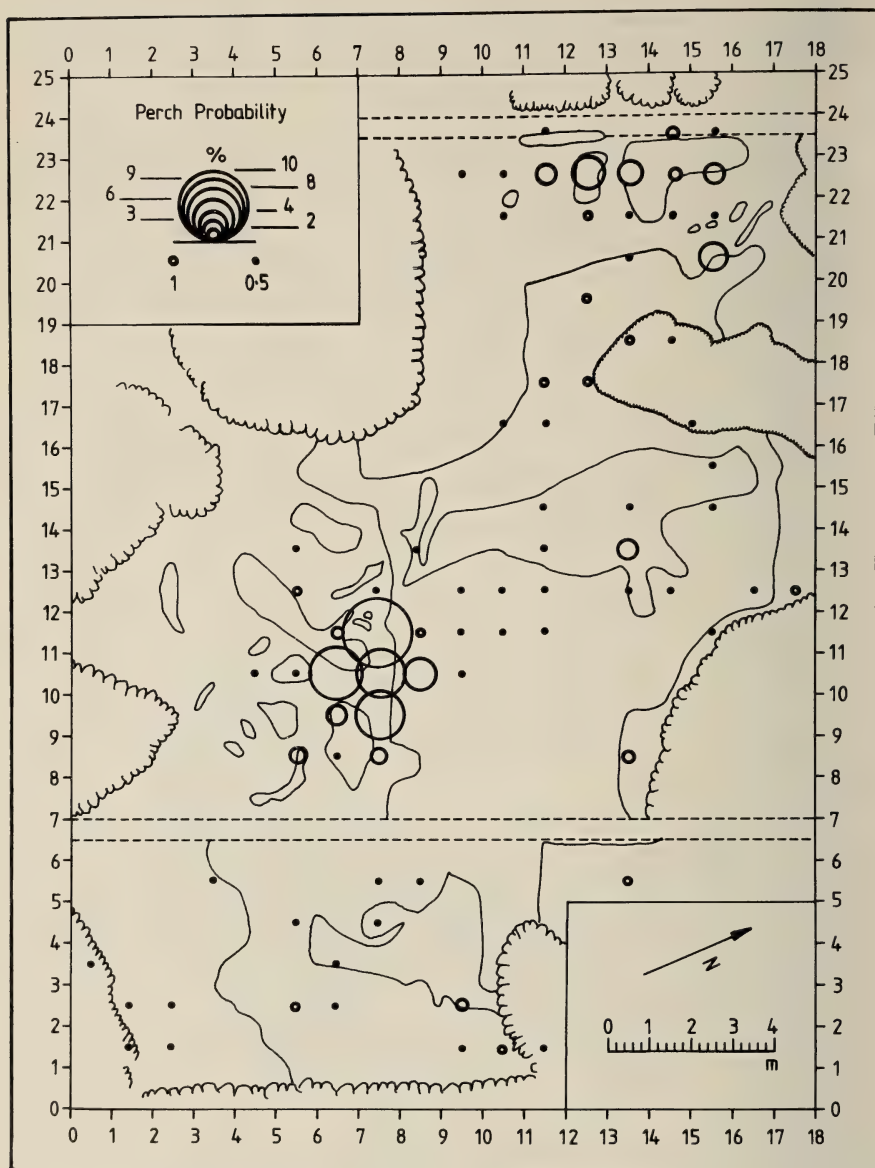
FIG. 5.   Probability distribution map for territorial male *O. venata*, based on 162 transects in clear conditions evenly spaced over 4 days, 30 June, 3, 7, and 23 July 1984 (6 transects/h). Two well established territories occur; the most important centers on map coordinate 0710, the second around 1422.
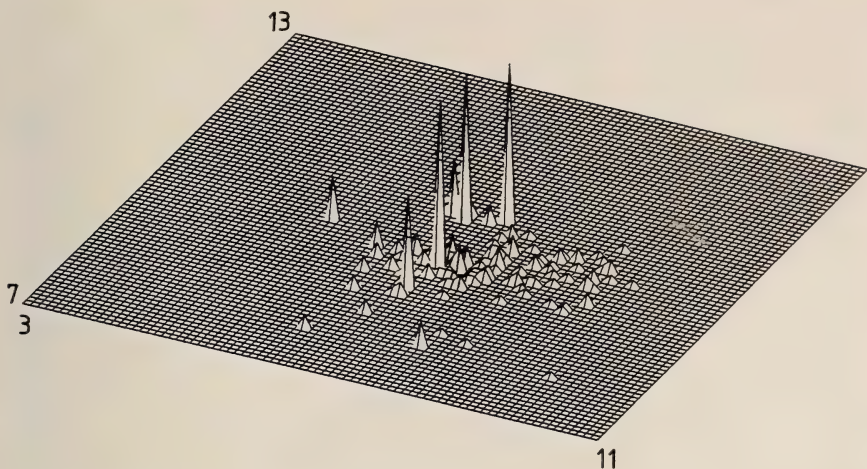
FIG. 6.   Fish-net plot illustrating relative frequency of different perch sites by territorial male *O. venata* in main territory of clearing (map grid reference 070100) based on 38 insects and 364 records (resolution 10 cm). The figures at the corners are map coordinates for Fig. 1.

Inside territories. There is a distinction between what can be labelled a territory (the area defended by each male) and perches within a territory (the platforms or sites used by males after each sortie or voluntary patrol in the area defended). Dominant among perches in the main territory of the clearing are tiny birch seedlings under 15 cm tall (the same height or lower than surrounding heather), corresponding to the six substantial peaks in the plot (Fig. 6). The multiplicity of residual "relief" relates to sprigs of heather or cross-leaved heath, even grass blades, casually used during voluntary patrols or after interactions.

The actual size and shape of the territory varies from individual to individual (Fig. 7) despite the fidelity of different insects from day to day and year to year to the main perches illustrated in Fig. 6. Many males are restricted to some smaller portion of the two territories in the clearing; in the central territory, to the E or W half separated by the bank of *Calluna*. Nevertheless, others use a wider array of perches, and the unified structure of the main territory is evident in the links joining the main perches in Fig. 7. Interactions between males lead to the discovery and use by incumbents of a wider array of perches. Thus, both the main territories in the clearing are too large for one *O. venata*; intruders can pass over a portion of the territory and temporarily settle in another part of it unnoticed. However, each territory is also too small for two or more *O. venata*. A sortie after intruders by one occupant usually triggers activity in the other. Once this happens, violent interactions occur, often repeatedly triggered by a third party, until one of
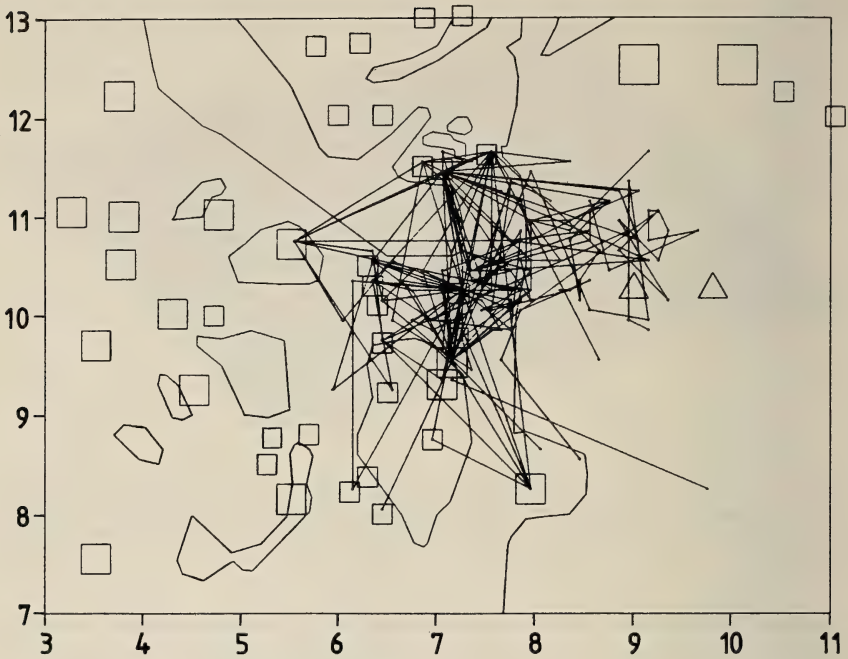
FIG. 7. Linkage diagram illustrating consecutive moves by male *O. venata* between perch sites in main territory of clearing around grid coordinate 0710. Zone covered by peaks in Fig. 6 represents a single territorial unit. Frequency of moves between perches is not illustrated. Data as in Fig. 6. Base map includes location of vegetation boundaries and tree seedlings (squares) shown in Fig. 1.

the two prior occupants leaves. Occasionally such premium is placed on the central territory that fourth and fifth males were noticed to enter while three contesting the zone are immersed in dispute. They, in turn, become incorporated in the next "dog fight".

The siting of territories has priority over perches, although shape and size of a territory can be distorted by altering the nature of perches within it. Males occasionally perched on artificial objects on the common, and used these repeatedly even if these "perches" were moved about. This effect is shown for the clearing where Fig. 8 illustrates perch sites adopted with and without a white plastic bag, alternated 4 times over 10 min periods. Clearly, the plastic bag disrupts the pattern of activity (Fig. 8, $\chi^2_{(1)} = 51.6$, P < 0.001) and acts as an overoptimal

$\longrightarrow$

FIG. 8. Linkage diagrams illustrating consecutive moves by male *O. venata* between perch sites in main territory of clearing; Top: in the presence of an artificial object (white plastic shopping bag). Bottom: in its absence. Triangles show two locations used for the artificial perch.
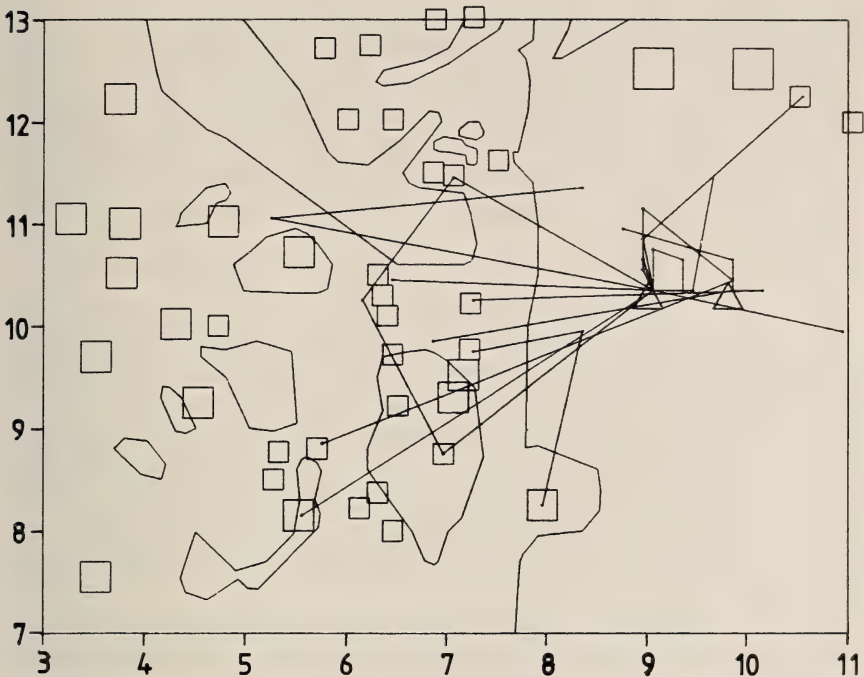
stimulus compared to the territory. There is, however, a limit to which territorial sites can be distorted. Artificial perches are used in the vicinity of sites where territories would normally be established, but apparently not in open areas usually ignored by the butterfly. At the woodland edge, the plastic bag was occupied continuously over 17 min of observation and contested for 13 times. In an adjacent wet heath area, it was visited twice by male *O. venata* during 11 min who inspected it while in flight and moved on.

Discussion

O. venata males reveal similarities and some differences with other butterflies that should complement the discussion on mate location behavior. Pertinent questions are: What determines the distribution of males? Why do they both perch and patrol? Why do they change their activities through the day, and how do they know when to change? Does the butterfly engage in territorial defense and, if it does, what factors induce the butterfly to defend one area more vigorously than another? How does it recognize good territorial sites and suitable perches in them?

Males are absent from the woodland cover and the dry heath. The woodland cover is dense, little light reaches the ground, and the butterflies would not be able to thermoregulate under it. The other negative zone, the dry heath, is void of nectar sources and lacks larval hostplants. Males are found in *Molinia* areas where there are eclosion sites, the most predictable locations for females. The enormous bias for bramble bushes points to a combination of factors: bramble is a major nectar source, and *Molinia* occurs in the immediate vicinity. Moreover bramble is typically associated with edge and junction sites.

O. venata perches and establishes territories in the early morning when air temperatures are low, and during the afternoon when they are highest. However, the insect treats afternoon as morning if the early part of the day has been cloudy and cool. In this respect, it is similar to vanessids in behavior, which also establish territories in the afternoon (Baker 1972, Bitzer & Shaw 1979, 1983), but differ from three satyrids, *L. meqera*, *P. aeqeria*, and *C. pamphilus*, which patrol more when air temperatures are highest (Dennis 1982a, Shreeve 1984, Wickman 1985a). Adoption of perching implies that a particular resource is more difficult to obtain. For one or more of several reasons, scrambling for the resource over a wider area becomes ineffective, and it is then necessary to wait for females at vantage points. The reasons are: (i) males have insufficient energy supplies to remain patrolling; more specifically, energy used in patrolling begins to exceed that used in defense (Baker 1972). (ii) Ambient conditions are inadequate for sustained flight, which lowers body

temperatures (Shreeve 1984). (iii) The ratio of available females is substantially reduced, and patrolling becomes less effective than perching at vantage points, regardless of energy resources. Energy losses during perching may match those of patrolling as skirmishing in territories can often be continuous and more violent than patrolling flights. Some territories are also occupied in the mornings, during the early and late flying season and in prime locations, presumably when energy levels are high.

Early morning perching may well relate, in part, to the need for both sexes to warm up and become fully active, but does not explain afternoon perching and mid-morning patrolling. On clear days, temperatures are higher after 1300 h than before. Perching as opposed to patrolling is more likely to relate to the unavailability of unmated females. It is possible that most unpaired females may be found by patrolling in the early part of the day, but that a switch to perching is effected in the afternoon as patrolling for a dwindling resource becomes unsuccessful. Whatever the explanation for switches in behavior, the reason is closely tied to the cue used by males to determine when switches are made. As neither energy nor ambient conditions (heat and sunshine) seem sufficient to explain the timing of switches in behavior, contacts (or lack of them) and scent may form prominent cues. The way males are arrested in flight to scan small areas for several minutes where nothing is to be seen suggests this. Clearly, more needs to be known about the influence of scent, particularly the distances over which behavior can be influenced by it.

Perching (and in some cases patrolling [Shields 1967]) has been likened to territoriality by Baker (1972) since defense of some "resource" is involved. This is denied by Scott (1974) for three reasons: (i) Males are incapable of learning topographic details of sites, and move on to new areas. (ii) As obvious resources are missing, there can be no territories for feeding, roosting, or oviposition. (iii) Interactions involve investigation of sex and not defense. Baker (1972), Davies (1978) and Dennis (1982a) have shown that males return to the same area repeatedly, even to the same perches, and that butterflies are capable of a spatial learning process (Baker 1978). We agree that species are genetically imprinted for characteristic topographic sites in which to establish territories (Scott 1974:107), but not for the precise details of sites, as insinuated by Scott. Scott's insistence that males should occupy the same area during several days does not hold in any case, since occupancy should be gauged against the time required to fulfill a particular function. Some perches are clearly established where there are female resources (hostplant sites in *A. urticae* [Baker 1972]; possible thermoregulation sites in *P. aegeria* [Parker 1978]; oviposition, therefore emergence, sites in *L. megera* [Den-

nis 1982a, 1986]). In *O. venata*, males have a bias for establishing territories where there is nectar in addition to the hostplant. Even where fundamental resources for females are missing, researchers have in every case shown that perches correspond to strong linear features or prominent visual markers, which have the capacity for concentrating resources. For virgin females, the most essential resource is males. Such strong visual lines dictate movement in insects and determine predictable locations for both sexes (Baker 1972, Dennis 1982a, Dennis & Bramley 1985, Shields 1967, Bitzer & Shaw 1979, 1983). Scott's own research has shown this to be the case in hilltopping males (Scott 1968) and for perching skippers (Scott 1973).

Finally, Baker (1972, 1983) has indeed shown that defense can be involved, and his observations are substantiated by others (Davies 1978, Dennis 1982a, Bitzer & Shaw 1979, 1983, Wickman & Wiklund 1983). In *O. venata*, perch sites are undoubtedly defended and are thus territories. Baker's (1972, 1983) observations are confirmed in that, usually, intruders failed to settle in an area unless the area was vacated, and unless escalated contests occurred when ownership was disputed. Two issues point away from Scott's insistence that territoriality in butterflies is no more than the investigation of the sex of the intruder by the incumbent and avoidance by the intruder of a would-be predator. First, interactions are significantly shorter between patrolling males; clearly it does not take long for males to determine the sex of individuals. Interactions between males at perch sites involve escalated contests back and forth over the perch site. Secondly, if the intruder is attempting to escape from a predator, it is then difficult to explain why it returns, often repeatedly, to the site to invite further strikes from the "predator". Despite these criticisms, it would be a mistake to regard the territorial defense (Baker 1983) and investigation (Scott 1974) models as mutually incompatible, although Scott's reasons for denying territorial defense are wrong. We suspect that the scale of defense is as variable as mate location behavior is flexible. At least three features point to an ability in *O. venata* to assess costs and benefits in defense: (i) the degree to which occupancy and defense varied between different territories in the clearing (corresponding to the premium placed on sites by males measured in numbers of intruders, length and violence of interactions); (ii) the varying degrees of pugnacity between contacting males when engaged in different activities (feeding, patrolling, and perching); and (iii) the voluntary abandonment of territories after unsuccessful periods.

Territories are typically established along distinct linear features, visual markers such as edges and junctions, but there is some indication that female resources may also be a factor in the location (as well as degrees of defense) of territories. Some sites, such as those in the clearing

(Fig. 5) associated with nectar sources, had territories throughout the morning on many days, but other sites along the woodland fringe associated with hostplant but without nectar were established only in the afternoon. Moreover, there was a distinct shift in location of the main territory in the clearing (Fig. 5) which coincided with changes in nectar apparency but not with temperatures. The varying frequency of perches in different parts of this clearing is in itself evidence of the varying quality of sites. However, not all hostplant locations and emergence sites become territories. Open areas, where females were found eclosing, were ignored. Visual rather than scent cues seem to be prominent in setting up territories.

Perching spots in territories are repeatedly used after interactions, but the fidelity to particular perches depended on the array of opportunities (number of potential perches) and the degree of disturbance by intruders, which usually led incumbents to cover a wider area and take up different posts. Typical perches were low, robust launching platforms providing effective observation posts. Taller seedlings over 1 m high were avoided, presumably because incumbents would then not be able to pick out intruders against the background vegetation beneath them. *O. venata* learns the spatial configuration of its territory quickly. Searches for artificial objects used as perches, removed during interactions, are first made where they occurred, the insects thereafter increasing the area searched. Voluntary patrols within the area of the territory probably contribute to gaining familiarity with territory landmarks. Several features then combine to demonstrate the adaptability of this hesperiid: opportunist behavior, spatial memory, ability to recognize resource-generating landmarks, and perhaps location of mates using scent—a developing theme in butterflies demonstrating degrees of "intelligence" in short-lived temperate species as well as tropical relatives with long-lived adults.

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THE STATUS OF "*PAPILIO HIPPARCHUS*" STAUDINGER (PAPILIONIDAE)

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ABSTRACT. The holotype male and only known specimen of "*P. hipparchus*" is critically examined for the first time since its description a century ago. Although traditionally accorded species status solely on the basis of Staudinger's original description and figure, this specimen in fact represents a morph of *Protesilaus phaon* Boisduval.

Additional key words: *Protesilaus phaon*, Colombia, taxonomy.

"*Papilio hipparchus*" Staudinger (1884) (type locality Cauca [Colombia]) has been one of the most confusing members of the "*lysithous*-related group" of swallowtail butterflies. Munroe (1961) placed this group in a subgenus of *Eurytides* Hübner. Hancock (1983) accorded the group generic status as *Protesilaus* Swainson. Irrespective of this difference, both authors included the following taxa: *asius* (Fabricius), *microdamas* (Burmeister), *thymbraeus* (Boisduval), *belesis* (Bates), *branchus* (Doubleday), *ilus* (Fabricius), *lysithous* (Hübner), *ariarathes* (Esper), *harmodius* (Staudinger), *trapeza* (Rothschild & Jordan), *xynias* (Hewitson), *phaon* (Boisduval), *euryleon* (Hewitson), *pausanias* (Hewitson), *protodamas* (Godart), *hipparchus* (Staudinger), *kumbachi* (Vogeler), and *chibcha* (Fassl). It has since been demonstrated that *illuminatus* (Niepelt), *dospassosi* (Rütimeyer) and *huanucana* (Varea deLuque) also belong to this group (Johnson et al. 1986a, 1986b).

Protesilaus hipparchus has been traditionally accorded species status solely on the basis of Staudinger's original description and figure of the type. This holotype (in the Staudinger collection at the Zoologisches Museum der Humbolt Universität zu Berlin [ZMH]) has not been examined by twentieth century students of Papilionidae (Rothschild & Jordan 1906, Jordan 1907, D'Almeida 1965, D'Abrera 1981, Hancock 1983). Based on original descriptions, Hancock (pers. comm.) speculated that *P. hipparchus*, *P. chibcha* and *P. kumbachi* represent aberrations.

As part of our ongoing review of some papilionid groups, and as aid to colleagues preparing a synonymic list of South American Papilionidae, we obtained the type (male) of *P. hipparchus* for study. It is described below, and dorsal and ventral surfaces, attached labels, and Staudinger's original figure are illustrated (Fig. 1) as well as relevant
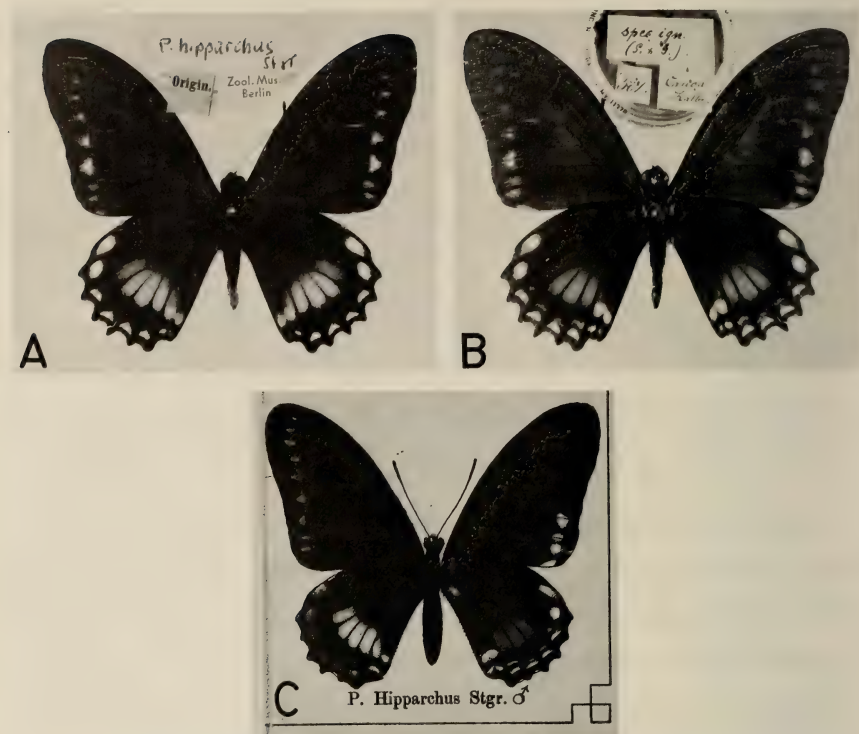
FIG. 1.   Recent photograph of holotype male *Papilio hipparchus* Staudinger. A, Upper-surface; B, Under-surface. C, Photograph of Staudinger's (1888) painted figure of *P. hipparchus* showing upper-surface on left, and under-surface on right.

genitalic characters (Fig. 2). Genitalic characters of *Protesilaus* have been reviewed in detail elsewhere (Johnson et al. 1986a, 1986b). As noted by these and other studies (Munroe 1961, Hancock 1983, Beutalspacher & Howe 1984), the valval harpe provides the most diagnostic characters.

The *Papilio hipparchus* Type
(Figs. 1A, B, 2A)

Length of forewing (base to apex): 40.5 mm.

Upper-surface of wings: Ground blackish brown. Forewing submarginal markings gray, hued slightly yellowish; hindwing submarginal markings gray, hued slightly yellowish, medial band very dull gray-white (faintly tinged with pink, a trait which might not be considered worthy of mention had it not been emphasized in the original description and subsequent interpretations of authors).

Under-surface of wings: Ground blackish brown. Forewing submarginal markings gray-white, hued slightly yellowish caudad; hindwing submarginal markings gray-white, hued slightly yellowish, a slight reddish slash in each cell costad to M1 and basad to each submarginal marking; medial band a slight lightening of ground color, becoming more obsolescent costad to M2 (Fig. 1B and C exaggerate extent of this lightness); two anal
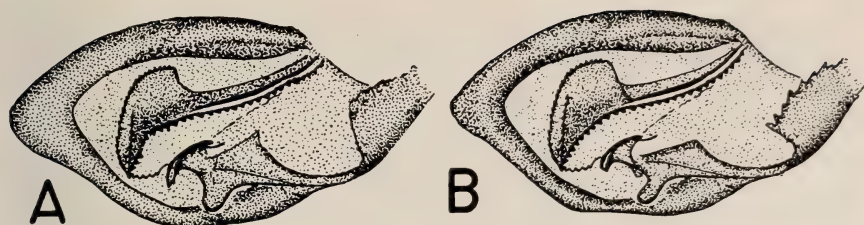
FIG. 2.   Diagnostic features of male genitalia of *P. hipparchus* holotype (A), and representative male of *P. phaon phaon* (Colombia, AMNH), after Johnson et al. 1986a, 1986b (B). Each shows inner-lateral view of right valve.

markings yellowish distad, reddish centrad. Traces of red occur at base of both wings along the thorax.
    Genitalia (Fig. 2A): Differing negligibly from nominate *P. phaon* (Fig. 2B).

DISCUSSION

The type of *P. hipparchus* does not represent a valid species, but rather, a morph of *P. phaon*. The genitalia are indistinguishable from *P. phaon*. *P. phaon* is highly variable as shown by the number of infraspecific names proposed for it (Rothschild & Jordan 1907:661–663, D'Abrera 1981:62). Early workers suggested that *P. hipparchus* should be associated with *P. euryleon*, probably as a sister species (Rothschild & Jordan 1906, Jordan 1907). This view probably resulted from Staudinger's original description. There he states that the accompanying figure is not accurate in all details, and that *P. hipparchus* lacks particular wing markings of *P. euryleon*, a species belonging to a monophyletic group that includes *P. phaon*, *P. pausanias*, *P. protodamas*, and *P. illuminatus* (Johnson et al. 1986a, 1986b, K. S. Brown, pers. comm.). Jordan (1907) and Rothschild and Jordan (1906) speculated that the inaccuracies of the original figure involved (a) the frequency of red-spotting in the anal area of the hindwing under-surface, and (b) the extent of the under-surface medial band. The degree of these markings could constitute major differences between the wing patterns of *P. hipparchus* and *P. euryleon*. However, as indicated in our description above, (a) the red on the under-surface is indeed nearly absent, and (b) the medial band (shown in the Staudinger figure as a brown band proceeding costad to the discal cell [Fig. 1C]) is actually a simple lightening of the under-surface ground color extending across the entire wing. In both of these features, the type of *P. hipparchus* resembles morphs of *P. phaon* more than those of *P. euryleon*. The major error in the original figure concerns the extent of submarginal markings on the forewing upper-surface. While the original figure shows these extending only slightly costad (Fig. 1C), they actually extend costad to the apex, where they are darker caudad.

We do not know whether this morph represents a natural population of possible subspecific status or a one-time occurrence. Were it not for slight yellowish tinges to submarginal wing markings, and the almost imperceptible pinkish flush to the upper-surface medial hindwing band, *P. hipparchus* might be considered a "black-white" morph of *Protesilaus*. Such black-and-white phenotypes are reported to occur as mimics of black-and-white-marked papilionids of the tribe Troidini (Young 1971, K. S. Brown, pers. comm.). They include such *Protesilaus* as *P. illuminatus* Niepelt (Johnson et al. 1986b), *P. harmodius* female form *viginia* Rothschild & Jordan (D'Abrera 1981), *P. phaon* male form *ulopos* Gray, and a tentative subspecies of *P. euryleon* from near Buga in the Cauca Valley of Colombia. Such mimicry probably also explains the unique black-white morph of recently described *Heraclides matusiki* Johnson & Rozycki (1986) (Papilionidae, Papilionini). Interpretation of *P. hipparchus* as not a black-white morph may follow only from the emphasis on red and yellowish markings in the original description, and its elaboration by subsequent authors without access to the type. There is no way to know if the type specimen has faded, but our experience indicates fading is unlikely. The type of Staudinger's *"Papilio diaphora"* (Johnson et al. 1985) is just as old, and suggests no fading when compared with recent specimens.

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A NEW WHITE-AND-BLACK SUBSPECIES OF *PROTESILAUS EURYLEON* (PAPILIONIDAE)

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ABSTRACT. *Protesilaus euryleon pleiades* (tribe Leptocircini) is described from the southern Cauca Valley of Colombia. The uniqueness of its completely white-and-black wing pattern is discussed in relation to other recently described taxa of *Protesilaus* and *Heraclides* (Papilionidae, tribe Papilionini) which apparently mimic white-and-black papilionids of the tribe Troidini.

Additional key words: *Protesilaus euryleon pleiades*, taxonomy, Colombia.

Attention has been drawn to neotropical papilionids of the tribes Papilionini and Leptocircini (*sensu* Hancock 1983) which display wing patterns primarily white over darker ground color (Johnson et al. 1986a, 1986b). Such phenotypes, distinctive among taxa usually showing red or orange-red hindwing markings, are generally attributed to mimicry of white-and-black colored taxa of the papilionid tribe Troidini (Johnson et al. 1986a, 1986b, Young 1971, K. S. Brown, pers. comm.). Our examination of examples of these white and dark mimetic morphs has led to increased recognition of their occurrence. *Heraclides matusiki* Johnson & Rozycki (1986) was described from NE Venezuela, and represents a distinctive cream-white-and-black taxon in the *anchisiades* species group (*sensu* Munroe 1961, Hancock 1983) (tribe Papilionini). *Protesilaus illuminatus* (Niepelt) (tribe Leptocircini), formerly known from one extant male syntype and an accompanying female (and not mentioned in the literature since its 1928 description) was collected again in 1981 and studied by us (Johnson et al. 1896b). This taxon, which we accorded species status because of its cream-white-and-black wing markings and distinctive genitalia, requires biological study to ascertain its relation to red-and-black morphs of the remaining species of the group. *P. illuminatus* might represent a biological subspecies of either *P. euryleon* (Hewitson) or *P. ariarathes* (Esper). In the *P. euryleon*-related species cluster of *Protesilaus* (which includes *P. illuminatus, P. euryleon, P. phaon* (Boisduval), *P. pausanias* (Hewitson), and *P. protodamas* (Godart) [Johnson et al. 1986a, 1986b, K. S. Brown, pers. comm.]) only the *P. phaon* male form *ulopos* (Gray) has been

recognized as a primarily white-and-black mimetic morph (D'Abrera 1981). In remaining *Protesilaus*, *P. harmodius xenaides* female form *virginia* (Rothschild & Jordan) is an example (D'Abrera 1981), and possibly also the type and only specimen of *P. hipparchus* (Staudinger). We have shown that the latter taxon represents a morph of *P. phaon* (Johnson & Matusik 1987).

During our study of the above papilionid groups, we obtained from the Calima River region of the southern Cauca Valley of Colombia fresh specimens of a completely white-and-black morph of *P. euryleon* (Fig. 1). The specimens are genitalically indistinguishable from *P. euryleon* (Fig. 2), but their wing patterns of pristine white on velvetine black differ from all known *P. euryleon* populations.

P. euryleon is exceedingly polymorphic (D'Abrera 1981:62–63, Rothschild & Jordan 1906:663–666). However, all previously known populations of the species show red coloration of the hindwing orbs, and most have prominent white to yellowish (or occasionally greenish) patches located medially on both surfaces of the forewing.

The value of the subspecies concept has been a source of controversy among lepidopterists, particularly regarding nearctic taxa (Murphy & Ehrlich 1984). In the neotropics, however, where mimicry phenomena abound (Sheppard et al. 1985), the concept has particular heuristic value and utility. Therefore, we apply the subspecies category to the recently discovered white-and-black southern Cauca Valley population of *P. euryleon*.

Protesilaus euryleon pleiades, new subspecies
(Figs. 1A, B, 2A)

Diagnosis. Distinguishable from all congeneric species-level taxa except *P. illuminatus* by the completely white-and-black wing markings except for minor reddish colorations as noted below. *P. illuminatus* has triangular-shaped white hindwing markings, not orb-shaped as in *P. euryleon*. *P. e. pleiades* has submarginal white coloration typical of the species, and lacks the prominent dorsal red anal marking of *P. illuminatus*. *P. e. pleiades* is distinct from other infraspecific white-and-black morphs of *Protesilaus* as follows: *P. h. xenaides* female form *virginia* (as characteristic of *harmodius*) has a complete medial line of small round spots on the hindwing upper- and under-surfaces (but white in form *virginia*); *P. phaon* male form *ulopos* (as characteristic of *phaon*) lacks the whitish medial patch on both forewing surfaces.

Description. Male. Upper-surfaces of wings: Ground color velvetine black. Forewing with bright white medial patch; hindwing with bright white orbs in vein interspaces from anal margin to caudad of vein M2; light white along margin at vein interspaces, more emphatic costad and bordered basad by extremely narrow red slashes in limbal area. Under-surface of wings: Ground color velvetine black. Forewing with area of mimetic patch powdered blackish over vague white; hindwing with markings as on upper-surface but slightly duller; however, red slashes are more emphatic basad of marginal spots and distinct at anal margin. Length of forewing: 41.0 mm (holotype); 40.5 mm (paratype). Female unknown. Male genitalia (Fig. 2A): Typical of *P. euryleon* as described by Johnson
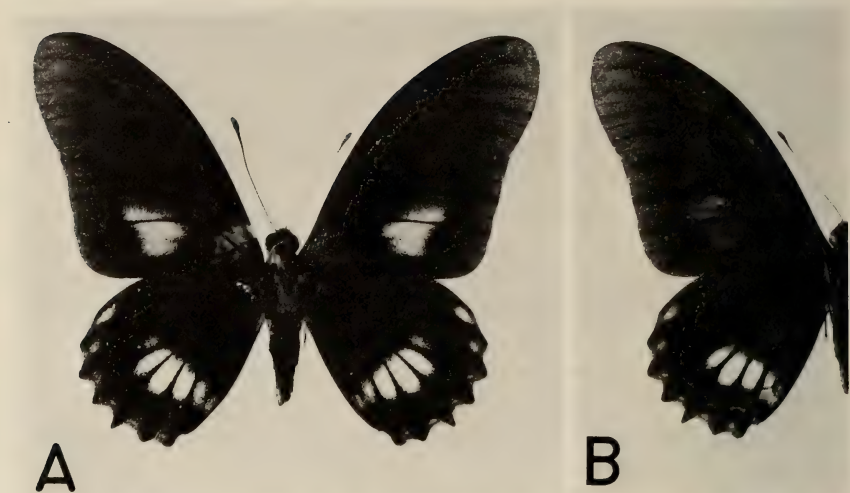
Fig. 1. Holotype male of *P. e. pleiades*. A. Upper-surface; B. Under-surface.

and Rozycki (1986) and Johnson et al. (1986b), differing only in more sharply pointed keel of valval harpe, and slightly larger ventral process (Fig. 2).

Types. Holotype male, on hillside above Calima River, 1,500 m altitude, 50 km SW of Buga, Cauca Valley, Colombia, 15 June 1983, leg. Phillip Mays, in American Museum of Natural History (AMNH); paratype male, same data, leg. local collector with P. Mays, in collection of Phillip Mays (Tarzana, California); paratype male, Rio Bravo, Calima River Valley [in Cauca Valley], June 1985, leg. Charles Condor, in collection of Rick Rozycki (Chicago, Illinois).

Distribution. Presently known only from the type locality, but possibly of wider distribution.

Remarks. Because we received the primary type and first-listed paratype specimens second-hand through an anonymous commercial dealer (who mentioned three other male specimens and provided conflicting collection data on different occasions) there was initial confusion about the precise location of the *P. e. pleiades* population. Earlier, K. S. Brown Jr. informed us he had heard reports of the population but did not know its whereabouts or the whereabouts of any specimens. Details were provided when we learned from Mays that he had personally participated in collecting the eventual primary type and one paratype. We assume the three other reported males (currently in the hands of the above-mentioned anonymous dealer) come from the same general area because Mays visited the type locality after being told that three other specimens had been collected there. Mays received this information from Christopher Farrell, a dealer who formerly resided in Colombia. Farrell reportedly remembered the general collecting data on the three specimens, though he did not keep them. The Cauca Valley data is further supported by the recent collection of the second-listed paratype. Considering the above, earlier data given us (and perhaps others) by the commercial source, citing the vicinity of Leticia, Amazonas State, Colombia, for *P. e. pleiades* specimens is probably inaccurate. Since these data derived from verbal communication, with label data available only in the case of the Mays paratype, we think the Leticia data were a miscommunication. *P. illuminatus* occurs N of Leticia in the upper Rio Putumayo Valley, and had also been obtained by us through the same commercial source; this may have caused the confusion. This background deserves mention because a white-and-black form of *P. euryleon* could foreseeably occur in the upper Rio Putumayo region, at the edge of its generally montane range.
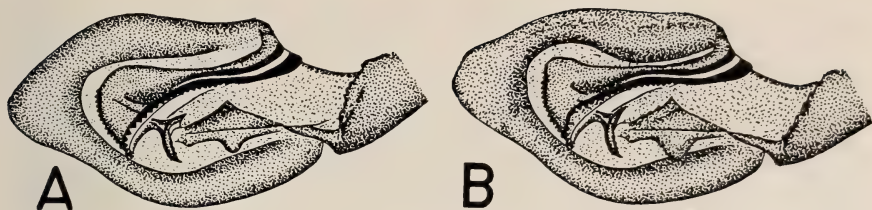
FIG. 2. Male genitalia of (A) *P. e. euryleon*, Costa Rica, AMNH, after Johnson et al. (1986a, 1986b) and (B) *P. e. pleiades* holotype. Each shows inner-lateral view of right valve.

Another papilionid known only from this region, *P. dospassosi* (Rütimeyer), also is distinctive in its reduction of upper surface red coloration (Johnson et al. 1986a).

Etymology. Following on the Greek binomial and referring to the bright white-on-black markings, *pleiades* (from the constellation of that name) denotes the seven-spotted pattern of the wing surfaces.

ACKNOWLEDGMENTS

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GENERAL NOTE

PREDATION ON ADULTS OF *ANARTIA FATIMA* (FAB.)

Additional key words: Nymphalidae, Costa Rica.

Vertebrate predation on adults can be a significant source of mortality in butterfly populations (Bowers et al. 1985, Evolution 39:93–103), yet the incidence of such predation has been documented in few cases. Although direct observations of vertebrate predation are rare (exceptions: Brown & Vasconcellos-Neto 1976, Biotropica 8:136–141; Fink & Brower 1981, Nature 291:67–70; Ehrlich & Ehrlich 1982, J. Lepid. Soc. 37:148–152), several studies have examined museum specimens or specimens collected during field sampling for evidence of bird predation (Carpenter 1941, Proc. Zool. Soc. Lond. A 1941: 223–231; Shapiro 1974, Am. Nat. 108:229–232, and others). Characteristic damage inflicted by birds (and probably lizards) includes symmetrical tears on the wings, straight cuts across major veins, triangular tears, and beak imprints (Sargent 1973, J. Lepid. Soc. 27:175–192; Bowers & Wiernasz 1979, Ecol. Entomol. 4:205–209). In general, unpalatable butterfly species have a higher incidence of beak imprints due to birds tasting the butterfly or remembering a previous bad experience and voluntarily releasing it (Shapiro, cited above; Bowers & Wiernasz, cited above). In contrast, palatable butterflies have a higher incidence of beak tears due to ripping their wings out of the bird's beak (Shapiro, cited above; Bowers & Wiernasz, cited above).

This study assessed the incidence of predation on adults of the common, palatable (Silberglied et al. 1980, Science 209:617–619) butterfly, *Anartia fatima* (Fab.) (Nymphalidae), at Finca La Selva Biological Station, Costa Rica.

Sixty *A. fatima* adults were collected in the grassy area near the laboratory at Finca La Selva and at "Rafael's house" by the river on 8 March 1986. The butterflies were stored in envelopes and later sexed and assessed for evidence of predation. Butterflies showing potential signs of predation were examined for characteristic indications of bird or lizard attack (Bowers & Wiernasz, cited above).

The sex ratio of our sample of 60 butterflies was 38 males and 22 females (1.7:1). Seven of the 60 butterflies (12%) showed clear evidence of predation, 6/38 males (16%), and 1/22 females (4.5%). Although there were more males damaged than females, the difference was not significant (Fisher Exact Test, $P_\alpha = 0.38$, power $[1 - \beta] = 0.21$ [Zar 1984, Biostatistical analysis, 2nd ed., Prentice Hall, New Jersey]). Four individuals had symmetrical damage on two hindwings (HW) only, and another showed damage on two hindwings and a forewing (FW), indicating that the individuals were attacked while the wings were held together. Two individuals showed damage on a single side, one on the right HW-FW, and the other on one FW, indicating that the butterflies were probably attacked while the wings were open (Bowers & Wiernasz, cited above) such as when basking or flying. These results suggest that most predation occurred while the butterflies were roosting, probably at dawn or dusk (Rawlins & Lederhouse 1978, J. Lepid. Soc. 32: 145–159).

Twelve % predation is similar to what has been found in some other butterfly populations such as *Cercyonis pegala* (Nymphalidae: Satyrinae) (Bowers & Wiernasz, cited above) and *Ascia monuste* (Pieridae) (Pough & Brower 1977, Am. Midl. Natur. 98:50–58). We were unable to distinguish damage potentially caused by birds or lizards, and both may prey on butterflies (Boyden 1976, Evolution 30:73–81; Ehrlich & Ehrlich, cited above; refs. in Bowers et al., cited above).

The damaged individuals we collected were those that escaped after being attacked. We found only beak tears on the wings, and no beak imprints, concordant with the known palatability of these butterflies to predators (refs. in Silberglied et al. 1979, Psyche 87: 219–260; Harrison & Crabtree, pers. obs.). Our small sample indicates that individuals attacked at the hindwings are more likely to escape, perhaps because of the fragility of these wings compared to the forewings. *Anartia fatima*, as a palatable butterfly, thus likely escapes by tearing its wings out of the attacking animal's mouth or beak. This would be an easy task if the butterfly were captured by the flimsy hindwings.

Results from this study, as well as that of Silberglied et al. (1980, above) indicate that predation on these butterflies is relatively common. Although we do not have information on the number of successful attacks by predators on *A. fatima*, its palatability to both vertebrate and invertebrate predators coupled with the incidence of damage suggests that such predation may be a significant source of mortality.

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OBITUARY

JOHN STEVEN BUCKETT (1939–1986)

John Steven Buckett was born 6 December 1939 in Oakland, California, and died of pneumonia in Davis, California, 16 January 1986.

Steve attended primary and secondary schools in Petaluma, California, and graduated from Petaluma High School in 1957. Following brief service in the United States Marine Corps, he enrolled in Santa Rosa Junior College in 1958.

Steve entered the University of California, Davis, in September 1960. He earned his Bachelor of Science with a major in entomology in January 1965 and a Master of Science in entomology one year later. While a student at Davis, Steve became a member of Phi Kappa Phi in 1966 and Sigma Xi in 1967.

Between 1967 and 1969 Steve was employed as a systematic entomologist with the California Department of Agriculture in Sacramento. He was a Life Member of the Lepidopterists' Society and served briefly as Treasurer in 1969.

Steve wished to complete his Ph.D. at Davis but deteriorating health prevented this goal. His interest in moths remained intense, and he continued to collect until 1984, even though his activities became restricted to his yard in Davis. Although his fingers were crippled by psoriasis, he still prepared specimens occasionally during most of 1985.

The door to Steve's house was never locked. Friends and visitors were always welcome, and especially so when conversation turned to natural history and, particularly, moths.

Steve is survived by his mother, Mrs. Bertha R. Buckett, and sister, Mrs. Patricia Moore, both living in Santa Rosa, California.

Although Steve had broad interests in the natural sciences, his many publications dealt mostly with millipeds and moths. The joint moth collections of William Bauer and Steve Buckett, and the extensive Buckett library, have been donated to the R. M. Bohart Museum, Department of Entomology at the University of California, Davis.

John Steven Buckett, 1963

NEW TAXA DESCRIBED BY JOHN STEVEN BUCKETT

The holotypes of these species are deposited in the R. M. Bohart Museum, Department of Entomology, University of California, Davis, California 95616, unless otherwise indicated.

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Cover illustration: Semilooping larva of the strange noctuid *Phyprosopus callitrichoides* on *Smilax*. Sketch by Mark Klingler, Carnegie Museum of Natural History. Suggested by John E. Rawlins.

ECOLOGICAL SIGNIFICANCE OF A POSTMATING DECLINE IN EGG VIABILITY IN THE TIGER SWALLOWTAIL

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ABSTRACT. The number of times that field-collected tiger swallowtail females had mated increased significantly with age. Mean number of spermatophores per female was 1.97, and 65% of the females had mated more than once. Egg fertility and viability were independent of the number of eggs a female had oviposited. Both parameters declined significantly with time for sequential samples of eggs from both hand-paired and field-collected females. Between 10% and 25% of field-collected females that carried a spermatophore and laid over 15 eggs produced no viable eggs. Fresh singly-mated females and worn multiply-mated females did not differ in egg viability, but singly-mated worn females had significantly lower egg viabilities. Thus, an additional mating may be advantageous for females that receive inadequate spermatophores or live for more than a week.

Additional key words: Papilionidae, *Papilio glaucus*, infertility, spermatophore counts, multiple matings.

Mating histories of female tiger swallowtails, *Papilio glaucus* L. (Papilionidae), as revealed by spermatophore counts, probably are documented better than for any other species of butterfly (Drummond 1984). Although the debate about the role of sexual selection in maintaining the female color polymorphism remains unresolved (Burns 1966, Pliske 1972, Platt et al. 1984), it is clear that multiple mating is common in this species. This is in contrast to suggestions on theoretical grounds that female butterflies should prefer monogamy (Wiklund 1977a, 1977b, 1982). Levin (1973) was unable to demonstrate experimentally a selective advantage for multiple mating in *P. glaucus*.

The maintenance of the color polymorphism in female tiger swal-

lowtails requires frequency-dependent selection or a balancing of se-
lection pressures (Burns 1966, 1967, Prout 1967, Levin 1973). The loci
that control it are on the sex chromosomes (Clarke & Sheppard 1962,
Scriber 1985). Dark-morph females benefit as Batesian mimics of the
unpalatable, aposematic pipevine swallowtail, *Battus philenor* (L.)
(Brower 1958). One subspecies, *P. glaucus canadensis*, which occurs N
of the range of *B. philenor*, has only monomorphic yellow females.
Both yellow and dark female morphs occur in the other two subspecies,
P. g. glaucus and *P. g. australis*, which are sympatric with the model,
and the relative frequency of the dark morph is correlated positively
with the abundance of the model (Brower & Brower 1962, Lederhouse
& Scriber 1987).

Burns (1966) documented a greater mean number of spermatophores
carried by field-collected yellow females than by dark females. He
suggested that sexual selection favored yellow females by shortening
the interval between emergence and mating. Yellow females would
also benefit if a single spermatophore were inadequate to fertilize all
eggs a female was likely to oviposit. However, subsequent spermato-
phore-count studies of other *P. glaucus* populations have not revealed
significant differences in spermatophore number for the two color morphs
(Pliske 1972, 1973, Makielski 1972, Platt et al. 1984). In addition, Levin
(1973) showed that a single spermatophore was sufficient to fertilize all
the eggs laid by *P. glaucus* females in the laboratory. This eliminated
preferential mating with respect to color as the balancing selective
pressure, but did not explain why roughly half of the females in these
studies mated more than once.

However, closer examination of Levin's data revealed that his ex-
perimental females averaged only about 113 eggs during 5.4 days. Both
Remington (1959) and Lederhouse (1981) observed declines with time
in the viability of eggs from singly mated females of other swallowtail
species. In the black swallowtail, *P. polyxenes* F., a decline in fertility
was detectable only after about 10 days and was independent of the
number of eggs laid (Lederhouse 1981). In the present study, our pur-
pose was to investigate the fertility and viability of eggs laid by *P.
glaucus* females with longer mating intervals than those in the study
by Levin (1973). In addition, we wanted to determine under what
circumstances a female would benefit from multiple matings.

MATERIALS AND METHODS

Samples of females were collected from several locations. The *P. g.
glaucus* used for determining number of spermatophores carried were
captured in Adams and Scioto counties, Ohio. The *P. g. canadensis*
were collected in several counties in north-central Wisconsin. These

females were assigned to one of four categories of wing wear when they were collected (Lederhouse 1978). After they died, field-collected females and a portion of hand-paired females were dissected, and the number of spermatophores was determined.

Laboratory-reared (lab) females were hand-paired once to field-collected (field) or laboratory-reared males. All females were set up in plastic boxes (10 cm × 20 cm × 27 cm) with a sprig of black cherry, *Prunus serotina*, under saturated humidity. The boxes were placed about 70 cm from continuously lighted 100-watt incandescent bulbs. Females were fed a mixture of 1 part honey to 4 parts water at least once daily. Most females were allowed to oviposit until death.

Eggs were collected and counted at two-day intervals except on weekends. Larvae were removed as they hatched, and the remaining eggs were monitored for 10 days after the last larva hatched. Because the green eggs of *P. glaucus* become mottled and then turn black as the embryo develops, eggs could be assigned to one of three mutually exclusive categories. Eggs were classified as infertile if they showed no development, inviable if they developed but did not hatch, or viable if they hatched.

Unless otherwise indicated, values are presented as means ± standard deviations. Since the lab-reared males and females were the offspring of mothers from a variety of locations, and since numerous combinations were mated, the Friedman two-way analysis of variance was used for the analyses of fertility and viability (Siegel 1956). Sequential samples from each female were ranked for both variables. A modified Tukey test was used for multiple comparisons of ranked samples (Zar 1984). Only females that laid eggs for at least three sampling intervals, produced at least 50 eggs, and had some eggs hatch were included in these analyses. In addition, each field-collected female with at least one spermatophore and that laid 15 or more eggs was monitored for egg fertility and viability.

RESULTS

Field-collected dark-morph females averaged 1.97 ± 0.90 spermatophores (Table 1). All had mated at least once, and 65.4% had mated more than once. The females were distributed uniformly across wear classes with a mean of 2.45. Mean number of spermatophores per female increased significantly with increasing wing wear (Table 1). The correlation between spermatophore number and wear class was highly significant (Spearman Rank Correlation, r = 0.52, P < 0.001).

Although the actual percent hatching was highly variable from female to female (Table 2), the pattern of decreasing egg viability was detectable by the end of the first week of oviposition. All laboratory-

TABLE 1.   Number of spermatophores contained by *P. glaucus* females collected in Adams Co., Ohio in relation to wing condition. z and P values are for one-tailed Mann-Whitney *U*-tests comparing the means for adjacent condition classes.

Condition		Number of spermatophores					z	P
	n	1	2	3	4	Mean		
Fresh	23	16	6	1	0	1.35	2.30	<0.02
Slightly worn	34	13	17	2	2	1.79	1.82	<0.04
Intermediate	29	7	12	9	1	2.14	2.18	<0.02
Very worn	21	1	8	8	4	2.71		
Total	107	37	43	20	7	1.97		

reared groups of females showed a significant decline for the first three samples of eggs (Friedman two-way analysis of variance, Table 3). When only females that laid eggs for four intervals were considered, again all groups of lab females had significant decreases in viability (Table 4). The reverse pattern occurred in the analysis of infertility. The only group without a significant infertility increase through three samples was the 1984 lab females paired with lab males (Table 3). All three groups of lab females had significant increases in infertility through four samples (Table 4). There was no discernible pattern for the inviable category of eggs, although one group had a significantly nonhomogeneous result. In sum, the decline in viability with sample resulted mostly from an increase in infertile eggs and was not clearly related to a change in the inviable class.

Since field-collected females were older and probably had laid some eggs before capture, it was more difficult to get samples of eggs for sufficiently long periods for analyses. Females from neighboring populations (northern Michigan, northern Wisconsin and so on) were grouped together without regard to year because there were few differences between years for lab females. The results for field females were similar to those for lab females. Females from both *P. g. glaucus* and *P. g. canadensis* populations showed significant declines in viability after three samples (Table 3). The decline was not significant for *P. g. canadensis* females with four samples each (Table 4). This probably represents random variability between the very low viabilities of the third and fourth samples (Table 2). The increases in infertility were significant for both groups for three samples and for *P. g. glaucus* for four samples. Again, there was no pattern in inviable eggs with sample. The significantly nonhomogeneous result for *P. g. canadensis* females with four samples was a decrease in inviable eggs from sample to sample.

The significant sequential decline in egg viability could be related to either the number of eggs that had been oviposited already or the

TABLE 2.   Average egg viability (percent hatching) for each of four sequential samples from *P. glaucus* females. Top values are means; lower values are SD. The first sample size (n_1) is for the first three means; the second (n_2) is for the fourth.

Group	n_1	n_2	Sample no. 1	2	3	4
1984 lab female– lab male	18	14	79.0 23.4	67.6 27.2	58.5 34.8	46.9 32.8
1984 lab female– field male	20	12	74.2 29.6	56.9 26.1	45.4 32.1	40.2 31.8
1985 lab female– field male	18	13	91.2 11.7	81.0 29.1	64.1 35.6	46.4 37.7
P. g. glaucus field females	21	11	87.8 17.7	70.1 26.8	50.9 39.6	37.0 41.1
P. g. canadensis field females	21	12	79.3 24.3	38.9 31.2	28.7 33.0	38.2 42.1

time interval since mating. To distinguish between the two possible causes, lab females were divided into those that laid fewer than 125 eggs and those that laid more than 125 in the first two samples. For lab females mated to lab males, the viability of eggs in the first two samples combined did not differ significantly for the two groups (Mann-Whitney U, P > 0.50, Table 5). In addition, viability of third-sample eggs was independent of the number of eggs previously oviposited by the females (Mann-Whitney U, P > 0.50, Table 5). For lab females mated to field males, egg viability was actually higher for females that had laid more eggs. The differences were significant for the first two samples combined and for the third samples (Mann-Whitney U, both P's < 0.05). Therefore, any decline in egg viability was not the result of females using up their supplies of sperm as they laid more eggs. The potential for a single insemination to fertilize a large number of eggs is illustrated by two females that laid 290 and 306 eggs within 5 days

TABLE 3.   Analyses for homogeneity for each category of eggs for three sequential samples from *P. glaucus* females. Mean interval is number of days between mating or capture and oviposition of the last sample. Probabilities are for a more extreme value of the Friedman two-way analysis of variance statistic.

Group	n	Interval (no. days) Mean	SD	P Viable	Inviable	Infertile
1984 lab female–lab male	18	6.9	1.6	0.05	n.s.	n.s.
1984 lab female–field male	20	7.7	2.1	0.01	0.05	0.05
1985 lab female–field male	18	7.9	2.0	0.01	n.s.	0.01
P. g. glaucus field females	21	10.0	2.6	0.02	n.s.	0.01
P. g. canadensis field females	21	8.3	2.7	0.001	n.s.	0.001

TABLE 4.   Analyses for homogeneity for each category of eggs for four sequential samples from *P. glaucus* females. Mean interval is number of days between mating or capture and the oviposition of the last sample. Probabilities are for a more extreme value of the Friedman two-way analysis of variance statistic.

| Group | n | Interval (no. days) | | P | | |
		Mean	SD	Viable	Inviable	Infertile
1984 lab female–lab male	14	10.3	2.7	0.001	n.s.	0.001
1984 lab female–field male	12	11.1	3.4	0.01	n.s.	0.05
1985 lab female–field male	13	11.8	3.0	0.01	n.s.	0.01
P. g. glaucus field males	11	12.5	2.8	0.01	n.s.	0.001
P. g. canadensis field females	12	10.9	3.4	n.s.	0.05	n.s.

after mating. The viabilities for these two clutches were 90.0% and 97.1%, respectively.

Lifetime oviposition was high for females in this study. Lab *P. g. glaucus* females laid an average of 181.2 eggs ± 77.2 (n = 36). Yellow- and dark-morph individuals did not differ significantly in number of eggs laid. Field-collected *P. g. glaucus* laid 141.1 ± 61.4 eggs (n = 21), and *P. g. canadensis* laid 130.0 ± 44.0 eggs (n = 23). These values did not differ significantly (*t*-test, P > 0.20), but both were significantly less than the value for lab females (*t*-test, P < 0.05 and 0.01, respectively).

Since the decline in viability was significant using the Friedman two-way analysis of variance, a multiple comparison analysis was applied to the ranked samples to determine which were significantly different from the others. Using a modified Tukey procedure (Zar 1984), a general pattern emerged. Females mated to lab males had fourth samples that were significantly lower in viability than the first two. In both groups of females hand-paired to field males, the first sample was significantly

TABLE 5.   Viability (percent hatching) related to number of eggs laid by *P. glaucus*. Females were grouped by oviposition during the first two sample intervals. Means for oviposition and viability are given for the first two samples combined and for viability for the third sample.

| Female group | n | No. of eggs | | Viability (percent hatching) | | | |
| | | | | Two combined | | Third | |
		Mean	SD	Mean	SD	Mean	SD
Lab female–lab male							
Less than 125 eggs	8	80.6	29.5	77.8	15.7	62.6	28.1
More than 125 eggs	10	176.4	19.7	69.6	29.5	55.2	40.5
Lab female–field male							
Less than 125 eggs	24	74.2	20.9	69.6	22.4	44.2	34.8
More than 125 eggs	14	173.5	59.1	84.6	13.3	71.4	27.7

higher than the fourth sample. This suggests that the declines occurred sooner in females that had mated with males that may have mated before. For field-collected *P. g. glaucus* females, the first sample was significantly higher than the last two for both three- and four-sample analyses. For *P. g. canadensis*, the first sample was significantly higher than the last two for three samples per female. Since field-collected females had mated some time before capture, this reflects the longer intervals between mating and completion of oviposition for these females (Tables 3, 4).

Not all matings produced high levels of fertility and hatching. A proportion of the field-collected females that contained at least one spermatophore and laid 15 or more eggs laid no viable eggs. In 1985, 21.4% of 28 Ohio *P. g. glaucus* females produced clutches with total hatching failure. In 1986, 21.3% of 89 Ohio females also produced no viable eggs. A similar sample of 28 *P. g. canadensis* females had a 10.7% total failure rate. Comparable results are illustrated by 57 hand-pairings using males collected in Adams Co., Ohio. In 5 cases (8.8%), no spermatophore was transferred. An additional 12 females (21.0%) with spermatophores laid fewer than 5 eggs. Nine pairings (15.8%) resulted in entirely infertile eggs even though a spermatophore had been transferred. The remaining 31 pairings averaged 62.4% ± 23.3% larval hatch. Thus, for hand-paired females that had a spermatophore and laid eggs, 22.5% produced clutches with total hatching failure.

An additional mating often had a substantial effect on the viability of eggs laid subsequently. The effect of additional matings on hatching rate was investigated by comparing the first samples of eggs from field-collected Ohio females that mated once and that mated more than once. Females that had total hatching failure were excluded. Fresh singly-mated females had a mean hatching rate of 64.2% ± 29.8% (n = 26) which was significantly higher than the 35.5% ± 28.1% of 5 worn singly-mated females (Mann-Whitney U, P < 0.05). Worn multiply-mated females had a mean hatching rate of 69.4% ± 27.0% (n = 14). This was not different from that of fresh singly-mated females but was significantly higher than worn singly-mated females (Mann-Whitney U, P > 0.30 and <0.05, respectively).

DISCUSSION

Analysis of spermatophore counts for the Ohio *P. g. glaucus* documents the highest mean value for any population of this species studied to date. Not only is the mean nearly 2 spermatophores per female, but the proportion (65.4%) of the females that had mated more than once is also higher than any other reports for this species (Drummond 1984). Burns (1968) reported a mean of 1.75 spermatophores per female for

one population and a multiple-mating percent of 63% for another population of *P. g. glaucus*. Number of spermatophores carried by Ohio females increased significantly with wing wear (age). This agrees with results of Platt et al. (1984) and helps to explain the only low mean spermatophore values reported for this species. Pliske (1972, 1973) reported means of about 1.15 spermatophores per female, but his samples of females were considerably less worn.

As Levin (1973) demonstrated, a single normal insemination is sufficient to fertilize all the eggs a *P. glaucus* female is likely to lay. Our study confirms this even for females that oviposited over 50% more eggs on average than those in Levin's study as long as they were laid within a week of mating. In addition, our experiments document the potential for the sperm of one mating to produce fertilities of over 95% for females laying 300 or more eggs. That one normal insemination is sufficient also generally agrees with reports for *Papilio zelicaon* Lucas (Sims 1979), *P. polyxenes* (Lederhouse 1981), and *Pieris rapae crucivora* Bsd. (Suzuki 1979).

In contrast to Levin (1973), however, we document two situations in which an additional mating would be selectively advantageous for a *Papilio glaucus* female. First, a particular mating by a female is not always effective in fertilizing eggs. Second, even for a highly effective mating, the viability of the eggs of singly-mated females declines considerably with time regardless of oviposition rate.

In *P. zelicaon*, a newly emerged male or one that has mated frequently produces an abnormally small spermatophore often with a low sperm count (Sims 1979). In our study, 22.5% of hand-paired females that had spermatophores and laid eggs had total hatching failure. Another 15% of hand-pairings with some eggs hatching resulted in viabilities of less than 50% for the first two samples of eggs. Between 10% and 20% of field-collected females carrying at least one spermatophore laid no viable eggs. Although the complete hatching failure of some field-collected females may have resulted from a decline in viability with the time interval between mating and oviposition in the laboratory, our results suggest that the failure rate for natural matings is considerable (Drummond 1984).

The potential for long-term sperm storage is present in butterflies. Females of several species of *Heliconius* are capable of laying fertile eggs over 4–6 month lifespans (Dunlap-Pianka et al. 1977) although they usually mated only once (Ehrlich & Ehrlich 1978). However, in relatively short-lived species such as various swallowtails the sperm supply does deteriorate fairly quickly. Remington (1959) noted that later samples of eggs from hand-paired *Papilio* females had low fertility. In *P. polyxenes*, this decline was time-related but independent of the

number of eggs that had been laid (Lederhouse 1981). In *Euphydryas editha* Bsd., a single mating was effective for only 7 to 10 days (Labine 1966).

Egg viabilities and fertilities of singly-mated tiger swallowtails decreased over time. Our results for *P. glaucus* appear at odds with those of Levin (1973). However, this is likely the result of the average lifespan of 5.4 days for the females in his study. There was a decline in fertility for this period in Levin's study, but it was not significant. Both male and female *P. glaucus* live up to two weeks in the field (Berger 1986, Lederhouse 1982, unpubl. data). The 7- to 13-day average lifespans of the females in our study are more representative of a proportion of the females in the field. Females of short-lived butterfly species in thermally limiting environments may not benefit from mating more than once (Wiklund 1977a, 1982).

Egg viability decreased more gradually throughout the first week for females mated to virgin males. Only the fourth sample was significantly lower than the first for these females. These values declined sooner and more if the males were field-collected. This suggests that these males provided smaller spermatophores, possibly as a result of depletion of fluids from a previous mating, as is the case for multiply-mating *P. zelicaon* males (Sims 1979). Since spermatophores much smaller than average do not produce a mating refractory period (Sugawara 1979), females in the field could correct deficiencies by mating an additional time. Indeed, 50% of the Ohio females in the two freshest wear classes that had mated more than once had a first spermatophore that was considerably smaller than average (R. Lederhouse unpubl. data).

Declines in egg viability were substantial for all groups of females amounting to a reduction to half the initial viability level by 10 days after pairing. Although an additional mating does not guarantee higher viability, multiply-mated worn females had significantly higher viabilities of their eggs than singly-mated worn individuals. The average viability values for multiply-mated worn females did not differ from those of singly-mated fresh females. For females that live more than a week, an additional mating could be very advantageous since it is likely to restore viability levels to average values. Females of *Pieris brassicae* L. and *P. rapae crucivora* typically mate a second time a week after the first mating (David & Gardiner 1961, Suzuki 1979).

The rate of mating failure in natural copulations (10–20%) and the decline over time in the viability of eggs fertilized by a single male combine to make the probability of remating important in the tiger swallowtail. Sexual selection by males for yellow females could provide a differential favoring this morph. The dark morph females should on average live longer because of their mimetic advantage. However, if

the additional eggs they might lay during this period are largely infertile resulting from lower or slower remating rates, the advantage of their greater longevity would be reduced. The importance of sexual selection in maintaining the color polymorphism in the tiger swallowtail will not be resolved using spermatophore count data alone because of the limitations of this technique. However, mating frequency clearly affects lifetime reproductive success in *P. glaucus*. Suggestions that female butterflies should mate only once (Wiklund 1977b) must be limited to short-lived species. In longer-lived species, selection should favor regular mating intervals or more effective sperm storage. Such factors warrant further investigation in long-lived species.

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DEMOGRAPHY OF THE UNSILVERED MORPH OF *SPEYERIA MORMONIA* IN COLORADO

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ABSTRACT. The demographies of unsilvered and silvered morphs of *Speyeria mormonia* do not differ greatly in a Colorado population with a very low frequency of unsilvered animals. The frequency of the unsilvered morph is on the order of that expected if the unsilvered morph were due to a recessive allele with fitness zero, which is maintained only by mutation. The lack of detectable difference between morphs in demographic parameters suggests, however, that other factors control the frequency of the polymorphism.

Additional key words: Nymphalidae, polymorphism.

The silver spots on the underside of the wings of *Speyeria mormonia* Edwards (Nymphalidae) consist of modified scales. These silver spots are absent in some individuals, being replaced by buff colored spots. The percentage of unsilvered morphs in a population varies substantially among populations (Remington 1956).

It is not known whether the silvered-unsilvered difference is actually heritable, although Remington (1956) speculates that it may be controlled by one autosomal locus. The frequency of the unsilvered morph in a population may therefore be determined by any of a number of factors, including mutation rate, natural selection, drift, and—if the dimorphism should prove to be due to environmental plasticity—environmental characteristics.

Even in the absence of genetic information, we can begin to understand something of the forces governing the frequency of the morphs in a population by comparing demographic parameters for the two morphs. This is particularly true for populations in which the frequency of one morph is extremely low. In such cases, an extreme discordance in demographic parameters for the two morphs would suggest that extreme selection pressures relating to the unsilvered and silvered phenotypes exist in the adult stage. In the particular population examined here, the frequency of the unsilvered morph is in the range of that expected if unsilvered is due to a recessive allele whose fitness is zero and whose frequency in the population is thus determined strictly by the mutation rate.

Here I compare demographic data obtained over four years for unsilvered and silvered morphs in a Colorado population of *S. mormonia*. Recapture rates and maximum longevities (indices of survival), dispersal, and sex ratio are compared for the two morphs. I also examine

yearly shifts in percentage of unsilvered morphs in the population. While the sample size of unsilvered animals is by necessity quite small in a population with such a low frequency of unsilvered morphs, differences in values for demographic parameters are expected to be dramatically large if mutation balanced by low adult survival yielding a fitness of zero is responsible for the unsilvered morph's low frequency. The results thus give a first indication of the type and extent of differences between the morphs.

MATERIALS AND METHODS

The study was conducted near Gothic, Gunnison Co., Colorado. The study area consists of fescue grassland (Langenheim 1962), sometimes bordered by stands of aspen or spruce. Elevation varies from 2880 to 2970 m. Most lower slopes face SW, while upper slopes face NW. The study area was divided into topographic sites for calculation of dispersal distances. Total area sampled in 1979 was 6.0 ha; in 1980, 24.7 ha; in 1981, 5.6 ha; and in 1982, 6.3 ha (see Boggs 1987 for further detail).

Standard mark-release-recapture techniques were used in this study each summer between 1979 and 1982. Date and time of capture, butterfly number, sex and site of capture were recorded. Captured individuals were immediately released at the site of capture. Recaptures of individuals on the same day in the same site were not recorded. Dispersal distances were measured between centers of sites.

RESULTS AND DISCUSSION

Frequency of unsilvered animals captured in this population varied between 0% and 0.2% (Table 1), and did not differ significantly among years (Table 2). In 1981, the one unsilvered animal caught had half of each normally silvered spot unsilvered.

If the frequency of unsilvered animals in the population were controlled by the mutation rate alone, with the fitness of homozygous recessive unsilvered animals equal to zero, then the square of the frequency of unsilvered would equal the mutation rate. Mutation rates for this population would therefore be 5.1×10^{-6} in 1980, 1.4×10^{-6} in 1981 and 4.7×10^{-6} in 1982, which are in the range reported for whole-locus mutation rates in *Drosophila* (Crow 1986).

Given a total density for this population of about 2000/ha, and an average dispersal distance of about 175 m (Boggs 1987), the lack of significant difference among years in frequency does not rule out genetic drift as a factor affecting frequencies of the morphs. For example, the time to fixation for a neutral mutant is approximately four times the effective population size (Crow 1986); the change in frequency in four generations under these circumstances would not necessarily be large enough to detect without a much larger sample size.

TABLE 1.   Number and sex ratio of silvered and unsilvered S. mormonia marked per year.

Year	Total no. silvered	Total no. unsilvered	Sex ratio	
			Silvered	Unsilvered
1979	590	0	3.7:1	—
1980	2646	6	3.6:1	1:1
1981	846	1*	6.2:1	1:0
1982	2762	6	2.4:1	5:1
Total	6844	13	3.2:1	2.2:1

* Half-silvered.

The sex ratio of unsilvered animals showed no consistent pattern (Table 1). Taken over all four years, the sex ratio of unsilvered animals did not differ significantly from that of silvered animals (Table 2). This is consistent with the hypothesis of determination of silvering by an autosomal locus.

Unsilvered individuals showed no pronounced difference from the silvered in other demographic attributes. Based on recapture frequencies for silvered animals (Boggs 1987), I expected to recapture 0.1, 0, and 0.2 unsilvered females in 1980, 1981, and 1982, respectively. None were ever recaptured. I expected to recapture 0.4, 0.1, and 1.8 unsilvered males in 1980, 1981, and 1982, respectively; 1, 0, and 2 males were recaptured in 1980, 1981, and 1982, respectively. The extremely close correspondence of these data to expectations over several years, in spite of the small numbers involved, indicates that survival and catchability of unsilvered individuals paralleled that of silvered butterflies among years. Ordinary statistical tests are precluded by the small numbers intrinsic to the situation. However, it is clear that, compared to silvered morphs, the unsilvered did not suffer massively greater mortality in the adult stage.

Maximum residence time is indicated by the interval between first and last capture. Maximum residence time in 1980 was 8 days for the one unsilvered male recaptured, whereas it was 15 and 28 days for the two unsilvered males recaptured in 1982. These values are not inconsistent with values for silvered individuals. For such butterflies, daily survival rates were lower in 1980 than in 1982, and maximum residence seen was 28 and 40 days, respectively, in 1980 and 1982 (Boggs 1987).

Dispersal characteristics of unsilvered and silvered morphs did not differ greatly either. The recaptured male in 1980 was recaptured in the same site as originally caught, yielding a dispersal distance of 0 m. Distances moved by the recaptured males in 1982 were 180 m and 580 m. Average distance moved by silvered morphs was about 175 m, with 60–80% of the recaptured animals dispersing (Boggs 1987).

TABLE 2. Tests of significance of differences among years in percentage of unsilvered morphs in the population, and of differences between morphs in the four year total sex ratio. The test statistic, x^*, Goldstein's (1964) exact binomial test for differences of proportions, equals the difference between the proportions divided by a pooled standard deviation, and is compared to values for t_∞. 95% confidence intervals for the difference between proportions indicate the amount of difference which could exist but not be detected as significant at $P = 0.05$.

Test	x^*	P	95% confidence interval for difference between percentages
Percentage unsilvered between years			
1979 (0%) vs. 1980 (0.23%)	−1.158	>0.05	−0.15% to 0.61%
1979 (0%) vs. 1981 (0.12%)	−0.835	>0.05	−0.16% to 0.39%
1979 (0%) vs. 1982 (0.22%)	−1.133	>0.05	−0.16% to 0.59%
1980 (0.23%) vs. 1981 (0.12%)	0.614	>0.05	−0.24% to 0.45%
1980 (0.23%) vs. 1982 (0.22%)	0.074	>0.05	−0.24% to 0.26%
1981 (0.12%) vs. 1982 (0.22%)	−0.573	>0.05	−0.24% to 0.44%
Percentage males between morphs			
Silvered (76.3%) vs. unsilvered (69.2%)	0.595	>0.05	−16.2% to 30.2%

There was thus no evidence for an extreme survival-residence disadvantage of the unsilvered morph. This is contrary to expectations if the frequency of the unsilvered morph is maintained by mutation in combination with an extreme selective disadvantage. However, the evidence presented here does not completely rule out maintenance of the unsilvered morph by a balance between mutation and selection, as, for example, ability to successfully lay eggs or mate was not examined.

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XANTHORHOE CLARKEATA (GEOMETRIDAE), A NEW SPECIES AND POSSIBLE ENDEMIC OF THE QUEEN CHARLOTTE ISLANDS, BRITISH COLUMBIA

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ABSTRACT. *Xanthorhoe clarkeata*, new species, of which 159 specimens were collected in 2 days in the Alpine Zone on Graham Island, is the first species of Lepidoptera reported only from the Queen Charlotte Islands. It is related to a holarctic species, *X. abrasaria*, but is easily distinguished by its usually reddish-brown coloring, greater color variability, strongly pectinate male antennae, and diurnal flight, as well as by genitalic differences. The new species may be a Pleistocene refugial relict. This aspect is discussed relative to what has been published on other endemic animals and plants of these islands, and on the biological evidence for a refugium there during the last glaciation.

Additional key words: taxonomy, biogeography, relict populations.

On a visit to the Queen Charlotte Islands, British Columbia, in July 1985, J. F. Gates Clarke of the U.S. National Museum of Natural History chartered a helicopter for two flights to the otherwise inaccessible mountains of the interior. His purpose was to investigate the Lepidoptera of the alpine tundra in these isolated ranges where no previous collections are known to have been made. One flight took him to 3100 ft (946 m) on a ridge near Mt. Brown, Graham Island, where he camped overnight. The other flight was a 1-day trip to a 3000 ft (915 m) ridge on Moresby Island. No butterflies and relatively few moths were present, but at the Mt. Brown locality a day-flying moth occurred in abundance. Dr. Clarke recognized it as something unusual, and he netted and pinned 159 specimens. Although virtually swarming above tree line on Graham Island, this species was not seen in similar habitats and under similarly favorable weather conditions on Moresby Island.

Comparison of these moths with all described North American species and subspecies and most palearctic species of *Xanthorhoe*, as well as with superficially similar taxa in other genera, leaves little doubt that it is undescribed. It is not a cryptic species but a distinctive one. I am pleased to name it after Jack Clarke, whose dedicated investigation of the Lepidoptera of the Queen Charlotte Islands led to its discovery and who collected all known specimens. Illustrations are by the author.

Xanthorhoe clarkeata Ferguson, new species
(Figs. 1–11)

Diagnosis. A variable day-flying species found above tree line on the mountains of the Queen Charlotte Islands, British Columbia. The most characteristic feature of the forewing pattern is the banding of the median space, in which the antemedial line is followed and the postmedial line preceded by fairly wide and regular light reddish brown to nearly

FIG. 1. Male genitalia of *Xanthorhoe clarkeata*. Aedeagus removed and shown in ventral view.

black bands that tend to constrict the much paler grayish central space between them. A small dark discal spot usually marks the center of what remains of the pale median space. Genitalia most resemble those of *X. abrasaria* (Herrich-Schaeffer) in general configuration, differing mainly in the shape or proportions of components, although one would hardly guess from external appearances that the two species were closely related. The usually reddish brown *clarkeata* has narrower, more pointed wings than the predominantly gray and black *abrasaria*, and its male antennae are bipectinate (heavily setose but not bipectinate in *abrasaria*). *Xanthorhoe clarkeata* is about the size of northeastern American *abrasaria* (subspecies *congregata* Walker). The forewing pattern, as well as the pectinate antennae, at first led me to compare *clarkeata* with the European *Scotopteryx peribolata* Hübner, but the genitalia are in no way similar.

Further description. Male antenna bipectinate, with black branches; longest branches about equal in length to 2½ antennal segments; ventral branches twice length of dorsal ones; branches conspicuously setose, shaft covered with brown scales to tip; female antenna simple, slender. Palpus rough scaled, light brown, exceeding front for about half its length, somewhat decumbent toward end. Front slightly convex, rough scaled, matching color of palpi; gena unscaled. Eye reduced to ⅕ width of front in male, ¾ width of front in female (width of eye equal to or greater than width of front in both sexes of *abrasaria*); eye finely and sparsely setose in both sexes. Chaetosemata large but not meeting mesially. Tongue well developed, dark brown, nearly black. Legs normal, fairly slender, with two pairs of hindtibial spurs in both sexes. Vestiture of legs and body a nearly uniform mixture of pale and darker gray-brown scales.

Wings appearing narrower than those of *abrasaria* because forewing is apically more
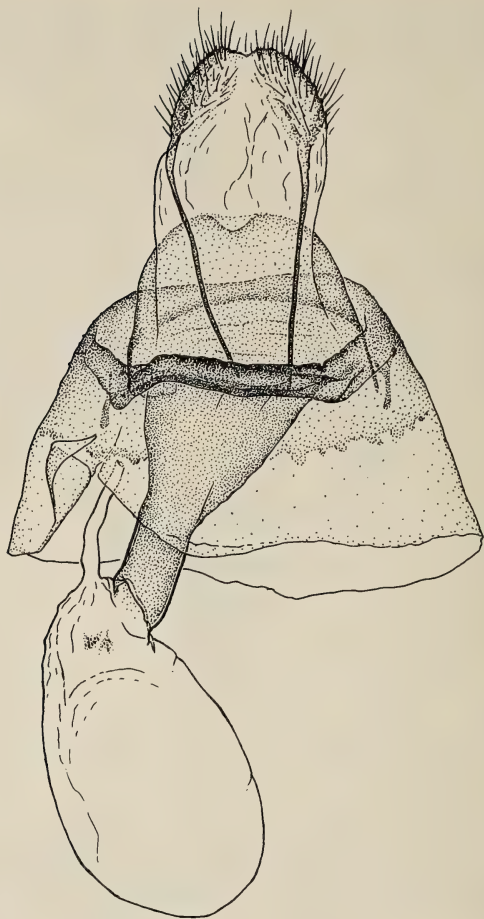
FIG. 2.   Female genitalia of *Xanthorhoe clarkeata*.

produced, that of female ending in slightly acute apex. Ground color of forewing pale bluish gray, but in nearly all males and some females this shade mostly obscured by darker gray-brown to bright reddish brown suffusion; pale basal and antemedial lines roughly parallel, convex, angled or bending inward toward costa, usually enclosing a grayish to rust-colored band contrastingly paler than basal band or proximal dark band in median space beyond; median space with its light-gray central area variably constricted by dark-brown to reddish-brown transverse bands that closely follow antemedial and postmedial lines; pale central area may remain a continuous medial gray band from costa to inner margin (Figs. 3, 9), be pinched off to form separate gray areas near costa and inner margin (Fig. 4) or one discal patch bearing the dark discal spot in middle (Fig. 7); postmedial line whitish, regular or slightly irregular but not as sinuous as that of *X. abrasaria*, convex near middle; dusky to rust-brown distal third of forewing often almost evenly divided by crenulate or dentate gray subterminal line parallel to outer margin; terminal line a series of double dark dots, one on each side of each vein; apex marked by small, oblique blackish dash directed toward or just behind apex. Hindwing darkened

FIGS. 3–11.   *Xanthorhoe clarkeata*. **3,** Holotype; **4, 5,** Male paratypes, 28 July 1985; **6, 7,** Male paratypes, 27 July 1985; **8,** Male paratype, 28 July 1985; **9–11,** Female paratypes, 27 July 1985.

by dusky suffusion, marked by faint discal spot, by diffuse pale postmedial and subterminal bands paralleling outer margin, and series of terminal dots like those of forewing. Fringes of both wings dusky to light gray or pale yellowish brown. Females usually much paler and more extensively grayish than males, although some are predominantly brown, and they usually have the light-gray median band of forewing unconstricted and much wider. Undersides of both wings dusky to reddish brown, with diffuse, darker postmedial bands with paler shading beyond, and often a diffuse subterminal, also pale-shaded outwardly. Length of forewing: holotype, 12.0 mm; other males, 11.0–14.0 mm (N = 144); females, 11.5–13.0 mm (N = 12).

Male genitalia (Fig. 1) (N = 2). Closest to those of *X. abrasaria* but with several conspicuous and numerous lesser differences; most notably: costa of valve with one or two dentate, subapical processes on inner side; membranous lobe of valve less ample, more flattened; costa of valve stouter, more heavily developed; large papillate process of juxta erect, recurved, not recumbent; saccus knoblike, rounded, not acuminate and pointed; manica more heavily spined than that of *abrasaria*; and vesica with similar two groups of cornuti, but distal ones longer than proximal ones, the reverse of *abrasaria*.

Female genitalia (Fig. 2) (N = 1). Differ from those of *abrasaria* in having larger, fully sclerotized ductus bursae about as long as bursa copulatrix, and with straight, transverse rim at ostium; a small signum only ¼ the size of that in *abrasaria*; better developed anterior apophyses 2 or 3 times as long as those of *abrasaria*; with integument of segments 7 and 8 dark pigmented, a difference often affecting the entire exoskeleton of diurnal moths.

Types. Holotype ♂, Ridge W of Mt. Brown, 3100′ [946 m], Graham Island, Queen Charlotte Islands, British Columbia, 27 July 1985, J. F. G. Clarke. Paratypes: 106 ♂, 12 ♀, same data; 38 ♂, 1 ♀, same locality and collector but taken 28 July 1985. Holotype and most paratypes in U.S. National Museum of Natural History; some paratypes distributed to American Museum of Natural History, Canadian National Collection, British Museum (Natural History), Los Angeles County Museum of Natural History, Queen Charlotte Islands Museum at Skidegate Mission, Graham Island, and other collections.

Remarks. In the description I compared *Xanthorhoe clarkeata* with *X. abrasaria,* a widespread, holarctic species with some obvious similarities in structure and wing pattern. The two are so easily distinguished by superficial features that I did not think it necessary to include figures of *abrasaria*. Illustrations of it may be found in Ferguson (1954:pl. 15, fig. 7), Morris (1980:pl. 29, fig. 10), and in many European works. An outline drawing of the male valve of *X. abrasaria* was given by Forbes (1948:148, fig. 158).

Biogeography

Xanthorhoe clarkeata is the first species of Lepidoptera to be recorded only from the Queen Charlotte Islands. Such a restricted distribution is unusual because most alpine and subalpine Lepidoptera in northern North America are more widespread. Many are holarctic. Although this species might still prove to occur elsewhere, it seems equally likely to be a local endemic or relict.

A few taxa endemic to the Queen Charlotte Islands have been recognized in other groups such as Coleoptera (Lindroth 1962:67), amphipod crustaceans (Bousfield 1958:64), and plants (Calder & Taylor 1968:102, 103, Schofield 1969:174). Endemism in the plants is regarded as surprisingly high, with four endemic species and seven well-differentiated subspecies, and all but one are limited to about the same alpine habitat as *X. clarkeata.* Although geological evidence has not been reassuring, biologists have long maintained that a Pleistocene refugium must have existed in the Queen Charlotte Islands (Calder & Taylor 1968:113, Schofield 1969, Randhawa & Beamish 1972). The concept that such a refugium persisted throughout the last (late Wisconsin) glaciation received new impetus from recent radiocarbon dating and analysis of plant remains in sediments and peat deposits by Warner et al. (1982), who showed that a diverse flora did exist near sea level on the E side of Graham Island 15,000 to 16,000 years ago and continuously thereafter. That was around the climax of the last glaciation, when the British Columbia mainland coast is believed to have been fully covered by glacial ice. The plant fossil deposits revealed the presence in the late Pleistocene of many of the same species that grow on the islands today, but some of them now only at higher elevations.

Considering the growing biological evidence for a refugium in the Queen Charlotte Islands, a few endemic species or subspecies of Lepidoptera were to be expected in addition to the previously known lycaenid, *Lycaena mariposa charlottensis* (Holland). Such an abundant and mobile species as *X. clarkeata* also might have spread back to the mainland in post-Pleistocene times, and I urge collectors to look for it elsewhere in the mountains of the N Pacific coast. The apparently endemic carabid beetle, *Nebria charlottae* (Lindroth 1962), has a close sister species in the Aleutians. Nothing comparably similar to *clarkeata* has yet appeared among the described and undescribed species of

Xanthorhoe from Alaska or the Aleutians, but those vast regions could hardly be described as well collected.

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A NEW SPECIES OF NEARCTIC *BOMOLOCHA* (NOCTUIDAE) FROM THE APPALACHIAN AREA

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ABSTRACT. *Bomolocha appalachiensis*, new species, is described from West Virginia, Kentucky and North and South Carolina. The type series consists of four males and seven females. The species is easily distinguished from known *Bomolocha* by forewing color pattern and male genitalia.

Additional key word: taxonomy.

Five specimens of a unique *Bomolocha* were taken in three West Virginia counties between 1977 and 1979. The species appears to be undescribed, and an additional six specimens were located in collections. Nothing is known of its life history.

Bomolocha appalachiensis, new species
(Figs. 1–7)

Description. Male. Palpi twice length of head, strongly curving upward to horizontal above antennal bases; laterally compressed, heavily clothed with flat scales dorsally and laterally, scales tan, tipped with dark brown; palps clothed ventrally with flattened hairs, dark brown, flecked with tan; third palpal segment small and white tipped. Antennae filiform, with white scaling at pedicel and dorsally on all segments. Vestiture of head dark brown with some light brown scales; frontal tuft strong and conical.

Vestiture of thorax and abdomen consisting of chocolate brown hairs and long flattened hairs mixed with elongated scales, concolorous with median area of wings. Basal tuft of thorax extending upward and strongly truncate. Abdominal tufts on segments 2–5, best developed on segments 3 and 4. Antemedian line of wings dark but not strongly contrasting, sinuous and slightly excurved at top of cell and in fold (Fig. 1). Postmedian line sharply defined, margined apically with pale scales, with smoothly rounded bulges at cell and at fold, the latter bulge stronger. Median area of wing darker, richer brown than basal area. A series of dots between veins represents subterminal line; most specimens with obscure subterminal dots. Some specimens with faint row of terminal dots between veins. Wing beyond postmedian line sandy to grayish brown, darker apically; paler costoapical triangle above. Hindwings medium brown or grayish brown with more luteus fringe and dark brown terminal line. Forewing length: 15.5–16.5 mm (N = 4); holotype male 16 mm.

Genitalia (Figs. 3–6). Uncus (Figs. 3, 4) long, slender, strongly curved apically. Valve flattened, evenly elongate and simple (Fig. 3). Anellus of aedeagus (Fig. 5) well defined and heavily armed with spicules. The everted vesica (Fig. 6) consists of two divergent lobes, one the ductus ejaculatorius, and the other a broad, shallow, evenly rounded blind pouch. On the side of the vesica below the ductus ejaculatorius is a small but well developed multitoothed cornutus. The blind pouch is densely clothed terminally with small cornuti. Below this cluster at the end of aedeagus is a second cluster of stouter cornuti.

Female. Similar exteriorly to male but with the following differences. Palps porrect, about three times length of head. Body vestiture shorter, much less dense than that of male. Antemedial line more faint; less contrast in color of basal and medial areas. Subterminal dots more developed. Two paratype females paler and less contrasting, with grayish lavender scales overlying tan shade beyond postmedian line. Orbicular visible as
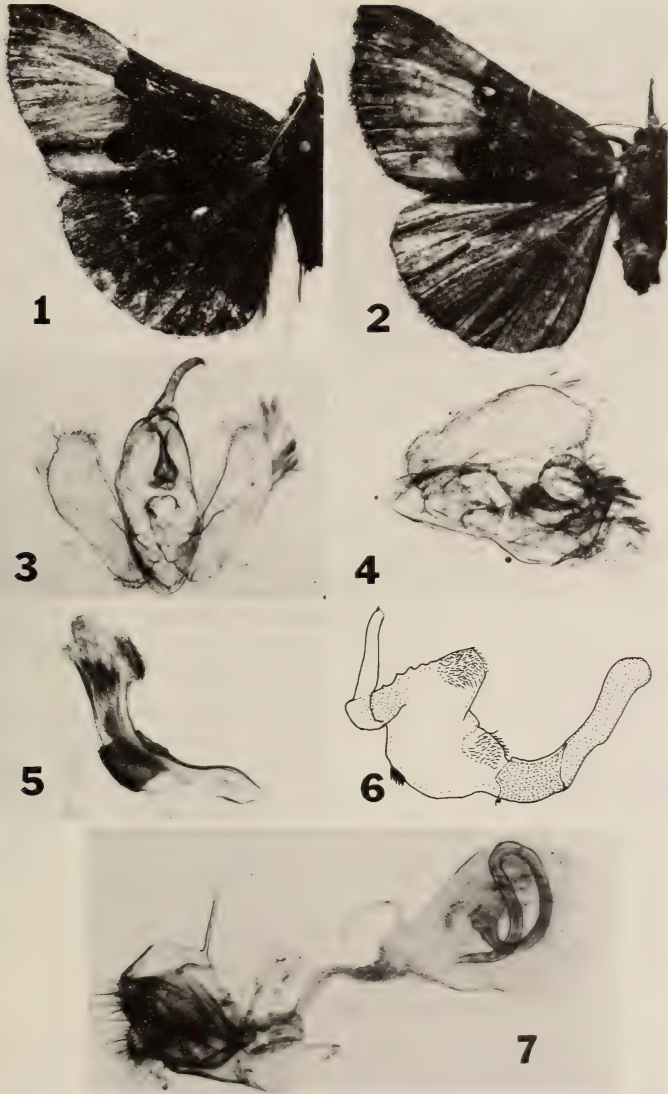
FIGS. 1–7. *Bomolocha appalachiensis*. **1,** Holotype male. **2,** Allotype female. 3–7. Genitalia. **3,** Holotype male, ventral view (aedeagus removed); **4,** Holotype male, lateral view (aedeagus removed); **5,** Holotype aedeagus, vesica not everted; **6,** Balsam Co., North Carolina, paratype, aedeagus, vesica everted; **7,** Allotype female.

a black dot in some females. Forewing length: 15–16 mm (N = 7); allotype female 16 mm.

Genitalia as illustrated (Fig. 7).

Diagnosis. Male genitalia of *B. appalachiensis* were compared with those of *B. manalis* (Walker), *B. baltimoralis* (Guenée), *B. bijugalis* (Walker), *B. palparia* (Walker), *B. aba-*

lienalis (Walker), *B. deceptalis* (Walker), *B. madefactalis* (Guenée), *B. sordidula* (Grote) and *B. edictalis* (Walker), the other *Bomolocha* species from the Appalachian region. Features of uncus, basocostal margin of valve, and sclerotized structures of aedeagus are diagnostic. Uncus of *palparia, madefactalis* and *sordidula* most similar to that of *appalachiensis* in being relatively long, slender, and curved apically.

Valve of *appalachiensis* simple. The basocostal corner on the inner face of the valve is more strongly protuberant or actually toothed in most other *Bomolocha* species examined; most species also show a slightly more distal projection. In *bijugalis* the valve is nearly as simple as that of *appalachiensis*, but the basocostal area is stouter and more heavily ridged than in *appalachiensis*.

Aedeagus of compared species of *Bomolocha* differs from that of *appalachiensis* in having clustered cornuti either more or less developed, and in lacking the multitoothed cornutus or having it well developed with an expanded base.

In size and shape of wings, *appalachiensis* is similar to *palparia* and *madefactalis*. Shape of the postmedian line, and degree of contrast between the chocolate brown basal two-thirds and paler apical area easily distinguish *appalachiensis*.

Types. Holotype. Male, Greenbrier State Forest, Greenbrier Co., West Virginia, 9 July 1977 at UV, Linda Butler (Fig. 1). Allotype. Female, Triune, Monongalia Co., West Virginia, 22 July 1979 at UV, Linda Butler (Fig. 2). Paratypes. 2 females, same data as allotype except 16 and 17 June 1979; 1 female, Big Ugly Public Hunting Area, Lincoln Co., West Virginia, 28 June 1979, Linda Butler; 1 male, Balsam, Jackson Co., North Carolina, 17 July 1974, Douglas C. Ferguson, U.S. National Museum Slide No. 56126; 1 male, 1 female, Oconee State Park, Oconee Co., South Carolina, 24 May 1973, Eric Quinter; 1 female, data as above except 15 August 1973; 1 female, Clemson, South Carolina, 26 May 1976, R. S. Peigler and J. W. McCord; and 1 male, Kingdom Come State Park, Harlan, Kentucky, 13 July 1984, Loran D. Gibson.

Holotype and allotype in U.S. National Museum; paratypes in U.S. National Museum, West Virginia University Arthropod Collection, and collections of Eric L. Quinter, Bryant Mather, and Loran Gibson.

Distribution. The localities given for the types represent the known distribution. All specimens were taken in the Southern Appalachian Mountains from Monongalia Co., West Virginia in the north to Oconee Co., South Carolina in the south.

Comments. Fifteen species of *Bomolocha* were previously known from North America (Hodges 1983). Besides the nine species found in the Appalachian region (Forbes 1954) and compared with *B. appalachiensis*, other species are *B. ramstadtii* (Wyatt) described from Florida (Wyatt 1967), *B. henloa* Smith described from Arizona (Smith 1905), *B. atomaria* Smith described from South Dakota (Smith 1903), *B. vega* Smith described from New Mexico (Smith 1900), *B. umbralis* Smith described from Florida (Smith 1884), and *B. variabilis* (Druce) described from Central America (Druce 1890). Woodruff (1913) discussed his collection of four specimens of *B. atomaria* from Connecticut.

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THE TYPES AND STATUS OF *PAPILIO TASSO* STAUDINGER

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ABSTRACT. Two syntypes, sole representatives of *Papilio tasso,* are critically examined for the first time and a lectotype male designated. The previously unexamined male genitalia are described and illustrated as well as the hitherto unillustrated syntype female. Lectotype wing characters and distinctive symmetrical valval harpes strongly suggest *tasso* is a valid species of the *torquatus* group of *Heraclides*. However, it should be investigated whether the lectotype represents a hybrid of common *H. torquatus* Cramer and nearly extinct *H. himeros* Hoppfer, and the syntype female an aberration or hybrid of the *H. polybius* Swainson complex.

Additional key words: taxonomy, Papilionidae, *Heraclides tasso.*

Papilio tasso has been one of the most enigmatic of swallowtail butterflies. The only known specimens, the male and female syntypes at the Zoologisches Museum der Humboldt Universität zu Berlin (ZMH), have remained unexamined by 20th century students of Papilionidae. Workers have either (a) retained *tasso* as a species based on Staudinger's (1884 [1888]) description and figure of the male (Rothschild & Jordan 1906, Jordan 1907, Munroe 1961, D'Almeida 1965, Hancock 1983), (b) questioned its status (K. S. Brown Jr. pers. comm.), or (c) suggested that the species might not exist (D'Abrera 1981). The *tasso* female has not previously been illustrated.

All workers have associated *tasso* with the *torquatus* group of *Heraclides* Hübner, including with it the following taxa (distributions from D'Abrera 1981, American Museum of Natural History [AMNH] and D. Matusik [DMC] collections): *H. himeros* (Hoppfer) (SE Brazil), *H. torquatus* (Cramer) (many subspecies from central Mexico to S-central South America), *H. garleppi* (Staudinger) (subspecies in W Amazon basin, Bolivia, and "Guianian region"), *H. lamarchei* (Staudinger) (Bolivia and SE Brazil, N Argentina), *H. hectorides* (Esper) (SE Brazil W to Bolivia and S to N Argentina). Most of these species (except perhaps *H. hectorides*) are considered rare, and are poorly represented in collections.

The sister group of the above taxa, the *Heraclides anchisiades* group, was recently reviewed (Johnson & Rozycki 1986). As part of an effort to clarify the status of terminal taxa in the *torquatus* group, we examined the *Papilio tasso* syntypes.
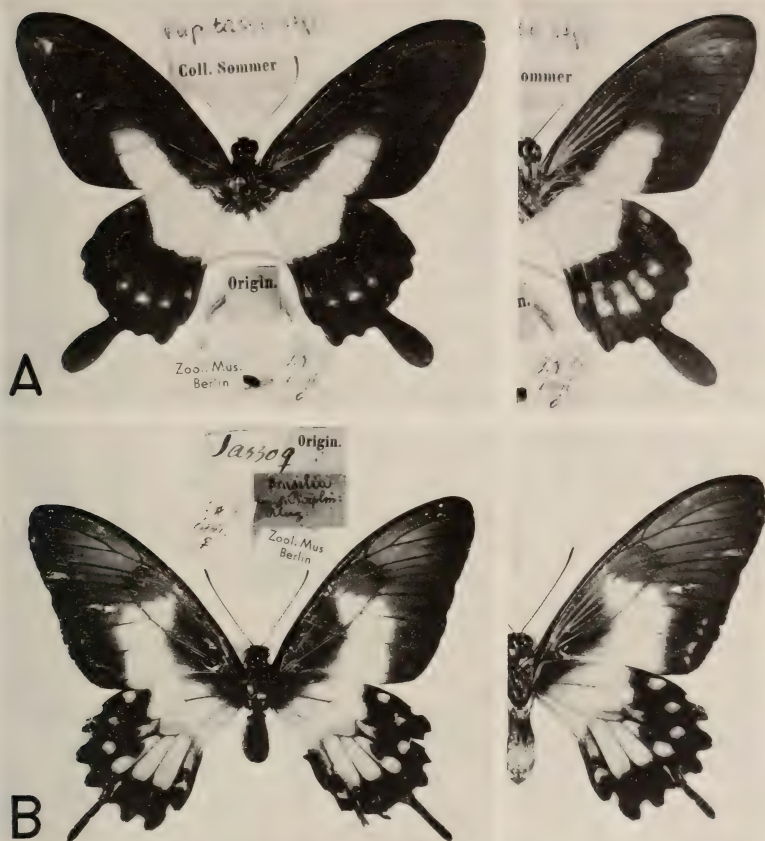
FIG. 1. *Papilio tasso*. **A,** Lectotype male; **B,** Syntype female. Upper surfaces at left, under surfaces at right.

Heraclides tasso (Staudinger)
(Figs. 1–2)

Papilio tasso Staudinger 1884 [1888]:19.

Types. Lectotype male (Fig. 1A) (ZMH) labelled "Origin", "Pap. tasso Stgr.", "Coll. Sommer", "Zool. Mus. Berlin" (no locality label, two undecipherable labels); we attached the label "lectotype designated by K. Johnson and D. Matusik, 1987"; locality by original description—"Brazil". Syntype female (Fig. 1B) (ZMH) labelled "Origin" "tasso female", "Brasilia", "Zool. Mus. Berlin" (two undecipherable labels). We designate the male as lectotype because precedent diagnostic studies utilize male genital characters, and incomplete collection data and other considerations leave doubt about conspecific association of the syntypes.

Characters. The lectotype differs from all other yellow and black members of the *torquatus* group as follows: **Wings.** Both forewing surfaces completely lack yellow coloration distad of median area; both hindwing surfaces lack basal black in yellow bands, broad yellow extending from median area completely to wing base; hindwing devoid of
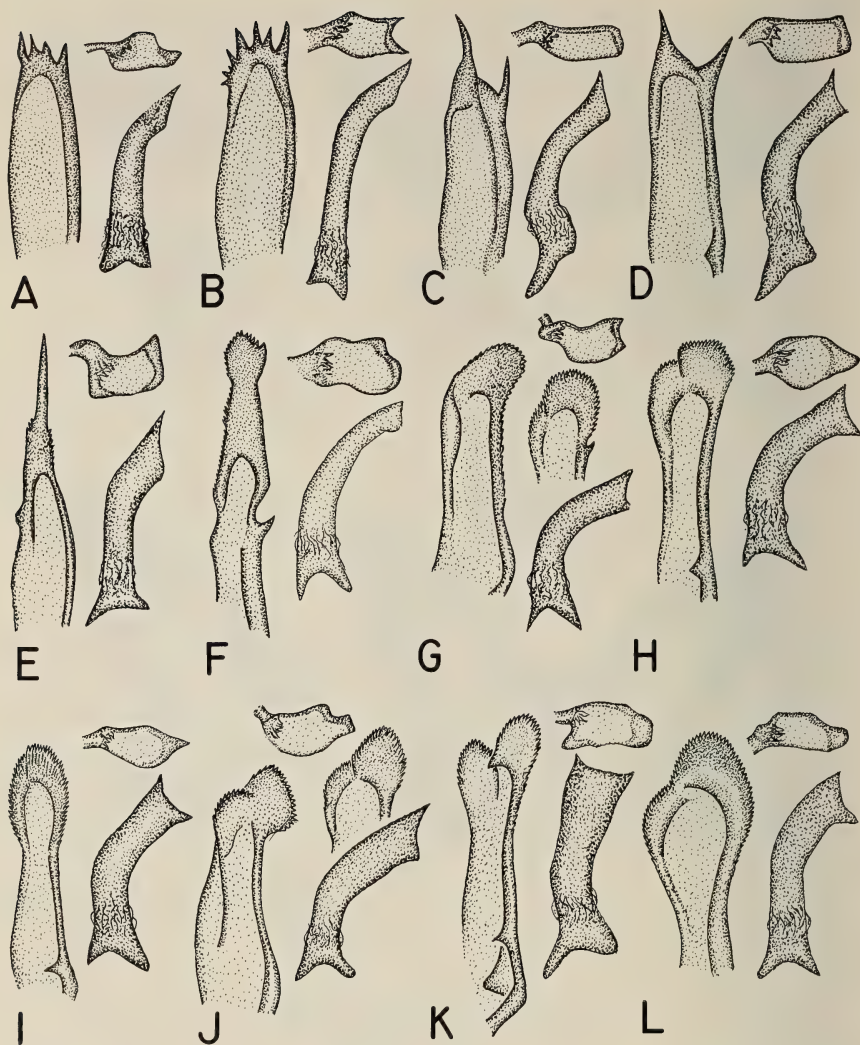
FIG. 2. Male genitalia of the *Heraclides torquatus* group, valval harpe, inner lateral view, on left; socii, outer lateral view, above right; aedeagus, lateral view, on right. Locality of specimen listed first with number dissected in parentheses if different than 1, additional localities and numbers in brackets thereafter. A, *hectorides*, Santissima-Trinidad, Paraguay (2) [Montevideo, Uruguay]; B, *lamarchei*, topotype, Bueyes, Bolivia [Agua Blanca, Argentina; Ichilio, Bolivia]; C, *garleppi garleppi*, "Bolivia" [Yapacani, E. Bolivia]; D, *g. interruptus* (Staudinger), Sani Beni, Peru [Tingo Maria, Peru; Carabaya, Peru]; E, *himeros*, "Mentor", Brazil [Bahia, Brazil]; F, *tasso*, lectotype; G, *torquatus torquatus*, Buena Vista, Bolivia [Teffe, Brazil], terminus of harpe above aedeagus, *t. polybius*, Matto Grosso, Brazil; H, *t. leptalea* (Rothschild & Jordan), Balzapamba, Ecuador (2); I, *t. orchamus* (Boisduval), Muzo, Colombia [Cauca Valley, Colombia]; J, *tolus tolus* (Godman & Salvin) (species status *sensu* Beutalspacher & Howe 1984), Chiltapec (Oaxaca), Mexico [Cordoba (Vera Cruz), Mexico], terminus of harpe above aedeagus, *tolus mazai* Beutalspacher & Howe,

emphatic postmedian to submarginal markings, these instead limited on under surface to three elongate whitish teardrop-shaped postmedian markings with adjacent smaller spots, and on upper surface to three small yellow spots, cells CU1 to M2; hindwing tails bulbously ovate; forewing length: 43.0 mm. **Genitalia.** Valval harpes symmetrical, each an extremely thin shaft terminating in a large serrate-edged knob; central area of shaft constricted and bearing a large, ventral-pointing spine; aedeagus with markedly constricted terminus. **Abdominal coloration.** Yellow over entire lateral area dorsad to thin black dorsal stripe, with cephalad-pointing black incised marking over lateral area of seventh and eighth tergites.

Status of *H. tasso* Based on Lectotype Male

Characters of the male valval harpe distinguish various papilionid taxa (Munroe 1961, Hancock 1983). We also showed useful differences in some aedeagii (Johnson et al. 1985, Johnson & Rozycki 1986). Figure 2 illustrates male genital characters of 14 taxa of the *torquatus* group. With the traditional species-level taxa are included eight taxa viewed by authors as subspecies of *H. torquatus*. Left and right *H. tasso* lectotype valval harpes are symmetrical and, compared with other members of the *torquatus* group, are very distinctive. By traditional taxonomic criteria (Munroe 1961, D'Abrera 1981, Hancock 1983), wing and genitalic characters of the lectotype strongly suggest that *H. tasso* represents a valid species. If so, its long absence from collections may reflect extinction or, as with *H. himeros*, near extinction (Collins & Morris 1985). Some workers, however, suspect that certain distinctive and rare papilionids result from infrequent hybridization (K. S. Brown pers. comm.). If this is true, distributional data and combinations of wing and genitalic characters suggest that *H. tasso* might be a *torquatus-himeros* hybrid. Such hybridization might explain the fuzzy limbal wing pattern and long, terminally knobbed valval harpe of the lectotype. Other characters, however, including the lectotype's symmetrical valvae, central harpe spine, bulbous hindwing tails, and lack of apical yellow do not appear to be easily explained in this manner. In one example of a rare papilionid "species" representing an unusual phenotype of another (Johnson & Matusik 1987), the genitalia of the aberrant specimen were nondistinctive.

Syntype Female of *P. tasso*

Association of the male and female *Papilio tasso* syntypes is problematic. As Staudinger noted, the markings of the female are compelling both as to uniqueness among *torquatus* group females and suggestion

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Guerrero (Guerrero), Mexico; K, *atsukaae* Igarashi, San Salvador, El Salvador; L, *tolmides* Godman & Salvin, Costa Rica. Dissections in AMNH and DMC except *tasso*. The last two are taxa of uncertain status.

of affinity to the male syntype. Workers who suspect *H. tasso* to be a hybrid suggest the syntype female may be an aberration of the non-yellow *H. torquatus polybius* Swainson complex (K. S. Brown pers. comm.). The syntype female resembles the lectotype in the extent and location of the white median to basal bands and in the bold lateral streaks on the under surface of the discal cell. Examination of *torquatus* group females in AMNH, DMC, British Museum (Natural History) (BMNH), Carnegie Museum of Natural History, Field Museum of Natural History, and Allyn Museum of Entomology indicates the syntype female is distinctive. Not only does it differ from congeners in the wing characters resembling the lectotype, but no other female specimen has extensive pink-orange on the hindwing or an abdomen almost completely white (congeners have a variably wide white lateral stripe). This extent of abdominal white is compatible with the extensive lateral yellow distinctive of the *tasso* lectotype and, to a lesser extent, males of *H. himeros*. Among *torquatus* group females, widening of the white forewing bands sometimes occurs in *H. torquatus* and *H. hectorides*. Usually, however, this widening does not include the discal cell, which is profusely invaded by white in the *tasso* syntype female. We know of no other specimen with basal to median white on the hindwing. A specimen of uncertain identification in BMNH labelled "Rio de Janeiro, Brazil" is similar to the *tasso* syntype female in wing and abdominal color characters except that it lacks basal to median white on both hindwing surfaces. We have not been able to ascertain if this is the same BMNH female cited by Rothschild & Jordan (1906:622) as bearing Gray's label "*P. polybius* 'variation a'" and appearing to them as synonymous with *H. tasso*. Original labels from Gray's curations apparently have not always survived. However, since the above female was segregated, it may be the same specimen. (We affixed a label to it, "*H. tasso*? . . .", referring to this paper.)

At present, study of the *H. tasso* female has limited value since females of the *torquatus* group are so rare in collections that the samples noted above would allow only comparison with *H. torquatus* and *H. hectorides*.

Conclusions

Traditional taxonomic criteria strongly suggest the lectotype of *H. tasso* represents a valid species. If so, it is possibly extinct or perhaps has not been collected since its original description. A number of "rare" papilionid taxa are known from only a few specimens (D'Abrera 1981, Johnson et al. 1985, 1986a, 1986b, 1986c); others have been collected only in disparate time periods (Collins & Morris 1985, Johnson et al.

1985, 1986b). Field and biological work must determine if extant natural populations exhibit the phenotypes of the *Papilio tasso* syntypes and whether their unique characters are attributable to hybridization or aberration.

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GENERAL NOTES

PUPAE OF *EURYTIDES THYASTES* AND OTHER LEPTOCIRCINE SWALLOWTAILS

Additional key words: Papilionidae, Leptocircini, Neotropics.

Immature stages of Neotropical kite swallowtails of the *thyastes* group (Rothschild & Jordan 1906, Novit. Zool. 13:726–734; Munroe 1961, Can. Entomol. Suppl. 17:17; Hancock 1983, Smithersia 2:20) are undescribed. In 1982 I obtained from Herbert Miers of Joinville, Santa Catarina, Brazil, four living pupae of the local member of the group, *Eurytides thyastes* (Drury), which he had reared. He told me that pupae of this species are sexually dimorphic in color, with green females and brown males, and indeed there were two of each sex and the colors were so distributed. It thus seems probable that pupal color in this species is not affected by the pupation environment, but, unlike the many examples of environmentally-cued pupal color dimorphism in swallowtails (Hazel & West 1979, Ecol. Entomol. 4:393–400 and others), green and brown pupae of *E. thyastes* are both dark and probably cryptic on the same substrates. The natural pupation sites are not known. *Eurytides thyastes* has a disjunct distribution: the upper Amazon region from NE Ecuador to Bolivia, and in SE Brazil near the coast (Rothschild & Jordan 1906, above). In Brazil the larval food is reported by Miers to be *Talauma ovata* A. St.-Hil. (Magnoliaceae), locally called 'baguaçú'. He reared the *E. thyastes* on leaves of this tree in October 1981. The species is univoltine in SE Brazil, and adults emerged in October 1982.

Fig. 1 shows a female pupa. Length 29.5 mm, widest point 9.5 mm, width of last abdominal segment 3.3. mm; thoracic horn about 2 mm long, projecting at 30° to the axis of the body. Green (female) and brown (male) pupae differ as follows: female green on all areas except where there is black (thoracic horn, dorsal surface of thorax, ventrally and dorsally on abdominal segments 4–6), pale tan (over wing bases, midventral region of abdominal segments 7 and 8, and in front of thoracic horn) or white (subdorsal mark on each side of abdominal segment 1). Ventral surface of last abdominal segment is brown, as are small tubercles on abdominal segments. Brown male pupae have exactly the same distribution of black, pale tan and white, but the green of the female is completely replaced by dull gray-brown. Among described leptocircine pupae it resembles *Eurytides epidaus* (Doubleday) (Ross 1964, J. Res. Lepid. 3:9–17), especially the head and the blunt thoracic horn, but *E. thyastes* is broader in the last few abdominal segments. The edges of the last segment are thick and dark. The pupa would merge with a thick branch if attached to one, much as *Papilio clytia* L. apparently does. Igarashi (1979, Papilionidae and their early stages, Tokyo [in Japanese] I:98) says that *P. clytia* pupates on branches at least as thick as a finger (translation), and it, too, has a broad tip on the abdomen (Igarashi 1979, above, II:color plate 107).

Both Munroe (1961, above) and Hancock (1983, above) place *E. epidaus* in the *marcellus* group, but its pupa differs in most respects from that of *E. marcellus* (Cramer). The thoracic horn of *E. marcellus* is pointed, and the pupa overall is smooth and patterned like the underside of a leaf, resembling those of some Old World *Graphium* spp. (Igarashi 1979, above). However, another member of the *marcellus* group, *E. marcellinus* (Doubleday), is, according to T. W. Turner (pers. comm.), "without any prominent projections".

In contrast, the *lysithous* group (*asius* of Hancock 1983, above) appears to be homogeneous in having bulbous green pupae with a long thoracic horn that continues the dark line on the side of the thorax and abdomen. Four members of the group are known to have this character: *E. belesis* (Bates) (Ross 1964, above, fig. 4A, B); *E. lysithous* (Hübner), *E. protodamas* (Godart) (West, unpubl. obs., specimens in Zoology Department, Universidade Federal do Paraná, Curitiba, Paraná, courtesy Prof. O. H. H. Mielke); *E. asius* (Fabricius) (H. Miers pers. comm.).

Apparently, pupae of the *protesilaus* group are undescribed, but that of one member of the remaining neotropical leptocircine group (*dolicaon* group) was described, though not figured, by D'Almeida (1924, Ann. Soc. Entomol. France 93:23–30): "Pupa 33 mm

Fig. 1. *Eurytides thyastes* female pupa. Left to right: dorsal, left lateral, ventral views.

long, 9 wide, conical, very elongate and slender towards the abdominal region, with a thoracic projection 7 mm long, triangular, horizontal, directed forwards and projecting over the cephalic region . . ." (D'Almeida 1924, above, D. A. West translation). Although sketchy, this description resembles something between *Graphium doson* (Felder) and *G. agamemnon* (L.) (Igarashi 1979, above, color plates 209, 213) and is quite different from *E. thyastes*.

In two related respects the pupae of *E. thyastes*, *E. marcellus* and *E. lysithous* are alike: the sculpturing of the posterior margin of the pupal hindwing has no "tail", and the developing adult tail within is folded back along the outer margin of the hindwing.

Pupal form may be a useful additional character for sorting out relationships in the Papilionidae. The limited data suggest that the *lysithous* group is monophyletic but that the *marcellus* group may not be. The comparison of Old and New World Leptocircini shows *Protographium*, *Lamproptera* and *Graphium* (Igarashi 1979, above), among the former, to be most similar to *E. marcellus* and perhaps *E. dolicaon*, among the latter. Hancock (1983, above) places the *thyastes* and *dolicaon* groups closest to the Old World genera and the *marcellus* group more distantly. Pupal morphology does not unequivocally support those placements, but the pupae of few species of Neotropical Leptocircini have been described.

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ROOSTING BEHAVIOR IN ADULT *VANESSA CARDUI*

Additional key word: Nymphalidae.

Nocturnal roosting behavior has been reported for many butterfly species, including *Heliconius charitonia* (Poulton, E. B. 1931, Proc. Roy. Entomol. Soc. London 6:71, and others), *H. erato* (Crane, J. 1955, Zoologica 40:167–197) and other species (Carpenter, G. D. H. 1931, Proc. Roy. Entomol. Soc. London 6:71; Clench, H. K. 1970, J. Lep. Soc. 24: 117–120; McFarland, N. 1971, J. Lep. Soc. 25:144–145). Below I describe apparent courtship activity and subsequent roosting for the night observed in *Vanessa cardui* L.

After a year of almost total absence in the Kalispell, Montana area (only one specimen seen in 1985), *V. cardui* was abundant throughout the Flathead River valley and the surrounding mountains in 1986.

In the Creston area E of Kalispell, the flood plain of the Flathead River consists of numerous sloughs and wetlands, many drained since the turn of the century. These are interspersed with remnant stands of spruce, and the sloughs are lined with cottonwood and other deciduous species. On 29 May 1986, Louis Nimeroff and I noticed large numbers of a medium-sized insect active around one cottonwood tree 18–19 m tall alongside the road, and about 30 m from any other tree. As it was shortly after 2100 h (MDT) and the sun had set, fading light did not allow us to identify the insects on the wing. Several attempts to net them failed, as they were flying rapidly about the tree, but eventually we succeeded, and found they were *V. cardui*. We stayed until flight ceased and available light was nearly gone. The insects seemed to be alighting on cottonwood leaves upon cessation of activity and roosting there for the night. We returned the following night for further observations.

On that evening, 30 June, we arrived at 2044 h and noted that the *V. cardui* were already engaged in the same activity as the evening before. Individuals were "chasing" close in to the cottonwood tree. Groups of 2 to 8 individuals "danced", flying rapidly in a circular motion around one another for 1 to 5 seconds, and then dispersed, each flying away in a different direction, although occasionally 2 or 3 would re-form into a new "dance" group and begin anew. This "dance" involved lateral as well as vertical displacement. At no time did any group fly vertically more than 4.5 m from the starting point before dispersing. This activity suggested courtship (Scott, J. A. 1985, The butterflies of North America, Stanford, California, p. 283) but attempts to net an entire group were not successful, and we were unable to determine sexual composition. At no time during the observation period, however, did we note mating.

Samples were taken opportunistically; nine males and two females were collected. All were worn, and were apparently new migrants into the area, although no obvious migration was noted. Fresh specimens did not appear in the area until mid-June.

Flight activity was observed up and down the tree, from ground level to the top. It was virtually constant, with individual insects pausing to rest on any convenient surface (ground, fence post, leaf, tree trunk, observer) for no more than 5 seconds. At rest, the wings were often held open so that the rays of the setting sun would fall full on them, but after sunset, which occurred at 2115 h, wings were held closed, and some were vibrated briefly in a manner reminiscent of sphingid and saturniid preflight warm-up. This thermoregulatory behavior has been noted elsewhere (Ferris, C. D. & F. M. Brown, eds. 1981, The butterflies of the Rocky Mountain states, Norman, Oklahoma, p. 31; and Scott 1986, above, p. 41). After sunset, resting became more frequent and prolonged.

Some individuals were noted chasing other flying insects that wandered into the area of activity, including a fly (Tabanidae) and a dragonfly. From time to time, an individual *cardui* would leave the area of the tree and fly into adjoining fields. Return activity was noted with about the same frequency, resulting in stability in the number of *cardui* active about the tree.

We checked the cottonwoods and other trees bordering the nearby slough, and noted *V. cardui* engaged in the same type of activity, but the insects were present at a lower density. The isolation of the cottonwood of our observations may well have acted to concentrate activity in its vicinity.

Activity ended abruptly. At 2148 h, flight and "dance" activity was still high. Two minutes later, only a few individuals were noted flying, and by 2154 h, all flight had ceased.

Individuals were observed flying into the tree and alighting on a leaf, where they remained at least as long as we could see them (until about 2200 h), and presumably passed the night there. All individuals observed (we estimate at least 100 insects present at any time) came to roost in the tree, but were widely dispersed, with no group roosting observed. We were unable to return to the site during the morning hours to observe dispersal for the day.

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OVIPOSITION BY *PARIDES ARCAS MYLOTES* (BATES) (PAPILIONIDAE) ON A GRASS LEAF-BLADE

Neotropical *Parides* oviposit exclusively on *Aristolochia* (Aristolochiaceae) plants (Moss 1919, Nov. Zool. 26:295–319; Cook, Frank & Brower 1971, Biotropica 3:17–20; Young 1973, Psyche 80:1–21; 1977, J. Lepid. Soc. 31:100–108; Brown, Damman & Feeny 1980, J. Res. Lepid. 19:199–226). Here I report a single observation of *Parides arcas mylotes* Bates ovipositing on the leaf-blade of grass.

At 1600 h on 28 July 1986, a "fresh" *P. arcas mylotes* was followed for ten minutes through the 10–20 cm high ground cover of grass and weeds in a small clearing within the cacao plantation "Finca Experimental La Lola" near Siquirres (10°06′N, 83°30′W; 50 m elev.), Limon Province, Costa Rica. The butterfly alighted on a 15 cm long *Aristolochia* sp. seedling partly concealed in dense grass, and placed one egg on a meristem leaf. The butterfly then flew around the vicinity of this vine, and returned a few minutes later and placed another egg on the leaf-blade of the grass *Acroceras zizanoides* (H.B.K.) Dandy (Graminae), about 25 cm from the *Aristolochia* (Fig. 1).

I collected both the *Aristolochia* and the *Acroceras zizanoides*, placing them in a tightly-closed plastic bag, to rear the two eggs. Roots of both plants were placed in a water-pik in the bag. I wanted to determine if the larva from the leaf-blade egg would feed on the grass, move to the *Aristolochia* vine (closest leaves about 10 cm away), or become disoriented and not feed at all. For the following two weeks of observation, neither larva fed on *Acroceras zizanoides*. The larva from the egg on the grass crawled to the *Aristolochia* without attempting to feed on the grass. Both larvae fed on the *Aristolochia*. I tentatively conclude that the oviposition on the grass leaf-blade was an aberrant behavior. Because troidine butterflies such as *Parides* are specialist herbivores on Aristolochiaceae (Brower & Brower 1964, Zoologica 49:137–159; and others), it would be of interest to determine the frequency of such behavior in the wild. Given that the meristem leaf of *Aristolochia* and the leaf-blade of *Acroceras zizanoides* are both narrow

FIG. 1. Top: Leaf-blades of the grass *Acroceras zizanoides* (H.B.K.) Dandy, and meristem leaves of *Aristolochia* sp., nonhost and host plants, respectively, for *Parides arcas mylotes* in Costa Rica. A second instar of *P. arcas mylotes* is on the ventral surface of the *Aristolochia* leaf. Bottom: Egg of *P. arcas mylotes* on the ventral surface of the grass leaf-blade.

and similar in shape (Fig. 1), suggesting they are visually similar to ovipositing troidine butterflies as shown by Rausher and Papaj (1983, Anim. Behav. 31:341–347), a fresh, "inexperienced" butterfly, like the individual observed here, might visually confuse host and nonhost plants. Nonhost oviposition occurs in the troidine genus *Battus* when the nonhost is visually similar to the host (Papaj 1986, J. Lepid. Soc. 40:348–349).

I thank D. R. Papaj for helpful comments and suggestions.

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MATING BEHAVIOR OF *ACRAEA ANDROMACHA ANDROMACHA* (FABRICIUS) (NYMPHALIDAE) IN NEW CALEDONIA

Additional key words: Acraeinae, sphragis, courtship.

Acraea andromacha andromacha (Fabricius) is reported from Australia (primarily N and E), the SW Pacific, and the Lesser Sunda Islands of Indonesia (Holloway, J. D. & J. V. Peters 1976, J. Nat. Hist. 10:273–318). It belongs to the mostly African subfamily Acraeinae (Nymphalidae) which feeds on Passifloraceae. The species is the only Australasian one of *Acraea*, and Passifloraceae occurs chiefly in the Neotropics and Africa (Heywood, V. H. 1978, Flowering plants of the world, Oxford Univ. Press, 335 pp.).

During copulation, male *Acraea* secrete a sphragis or plug and deposit it externally, thus preventing multiple female matings (Eltringham, H. 1912, Trans. Roy. Entomol. Soc. London, pp. 1–374). A large sphragis is believed to prevent mating by blocking the release of pheromone (Eltringham, above) and by the male detecting the sphragis physically (Scott, J. A. 1972, J. Res. Lepid. 11:99–127; for a review of the role of the sphragis, see Drummond, B. A. 1984, pp. 291–370 *in* Smith, R. L., Sperm competition and the evolution of animal mating systems, Academic Press). Common and Waterhouse (1972, Butterflies of Australia, Angus & Robertson, Sydney, 498 pp.) report the presence of the sphragis on Australian female *A. A. andromacha*. The sphragis is also known in other Acraeinae (*Planema* and *Actinote*), Papilionidae, and Danainae (Scott, above).

Along with the sphragis, African species of *Acraea* and *Planema* and *Parnassius* spp. lack courtship rituals (Eltringham, Scott, above). Strong female pheromones are postulated to replace courtship for intraspecific recognition (Eltringham, Scott, above). This mating strategy (assuming the pheromones exist) may have evolved where congeneric species of similar appearance and courtship occur sympatrically, as in African *Acraea*. Because *A. andromacha* is geographically isolated from congeners, it is not faced with interspecific mating.

This note confirms that *A. a. andromacha* has mating behavior typical of its congeners, presents evidence of multiple mating, and discusses possible gene flow effects resulting from single mating in an island environment.

In New Caledonia, *A. a. andromacha* occurs commonly in open, dry habitats with secondary vegetation and *Acacia* scrub (Holloway & Peters, above). Its external appearance and fluttery slow-wingbeat flight are reminiscent of *Parnassius* species (Papilionidae). I observed mating of *A. a. andromacha* on 28 January 1984 5 km N of Nepoui on the W coast of New Caledonia. The site was dominated by *Leucaena leucocephala* (Lam.) Dewit, an introduced legume-shrub found throughout the Pacific that occurs naturally in tropical America. The *Acraea* and other butterflies (*Junonia villida calybe* [Godart], *Anaphaeis java persithene* [Boisduval]), and an arctiid moth (*Utetheisa* sp.) were nectaring on *Tridax procumbens* L., a weedy roadside composite. At 1100 h, a male *A. a. andromacha* pounced on a female in flight, and seconds later, on the ground, climbed on her dorsum and copulated without a courtship dance (Figs. 1, 2). When disturbed, the pair flew, *in copula*, to a nearby *Tridax* flower. Although I did not observe which sex flew, the female presumably carried the male because she alighted on the flower. In some *Acraea* species, either sex flies, whereas in others the male or female flies (Scott, above).

I found sphraga on 14 of 15 female specimens, 1 per specimen, collected by M. G. Pogue and me in New Caledonia; and on 10 of 12 in the U.S. National Museum from Australia (8), New Caledonia (2), and the New Hebrides (2 without sphraga). Spermatophore counts were made on three New Caledonian specimens with sphraga and one without. Two of the three with sphraga showed evidence of multiple matings, with two partially dissolved spermatophores, while the remaining specimen with a sphragis had a single fully formed spermatophore. The specimen without a sphragis had no spermatophores, indicating, along with the excellent condition of her wings, that she was virgin.

FIGS. 1, 2.   Mating behavior and copulation in *Acraea a. andromacha*. **1,** Male climbs on dorsum of female and without courtship begins copulation. Wings of male nearly closed, pointing toward viewer, right wings more visible than left. Female's right hind wing positioned in front of her right forewing. **2,** Male's wings, now open, cover all but female's forewings, which are positioned beneath male's hindwings.

Multiple female matings, indicated by more than one spermatophore, have been reported in several other *Acraea* species (Owen, D. F. et al. 1973, Entomol. Scand. 4:155–160). They may be explained by loss of the sphragis due in part to its solubility in water, or by a second mating while the sphragis is still soft (Drummond, above).

Number of matings between individuals can affect gene flow between Lepidoptera populations. A female that mates only once, before migration, increases gene flow by transporting both her and her mate's genes to a new environment (Scott, above). In contrast, a female that mates again after migration lessens gene flow because the latter male fathers her subsequent offspring (sperm precedence, Labine, P. A. 1966, Evolution 20:580–586).

Sphragal-induced monogamy is more common in mainland areas, and one would assume that it has less adaptive value on islands. Nonetheless, such monogamy may serve to replace genes removed by natural selection from isolated island populations. Mated female *Acraea a. andromacha* with persistent sphraga (preventing further matings) and vagility equal to unmated females would influence gene flow among populations on Pacific islands more than unmated females. However, occurrence of multiple spermatophores in *Acraea* reported above and in the literature does not support this hypothesis.

McPherson of the Missouri Botanical Gardens for local arrangements in New Caledonia and identification of the plants; and J. A. Scott, and D. H. Clayton for critical comments on the manuscript.

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A MIGRATORY FLIGHT OF THE CALIFORNIA TORTOISE-SHELL BUTTERFLY

Additional key words: *Nymphalis californica*, Nymphalidae.

While migrations, swarms, and dense clusterings of butterflies are well documented, we believe any significant mass movement of a lepidopteran should be reported. Ultimately, published reports will form the basis for a clearer understanding of the conditions causing migrations. With such an objective, we here present field observations and data by one of us (RMK) of a unidirectional mass movement of *Nymphalis californica* (Boisduval) (Nymphalidae), the California tortoise-shell butterfly. This insect is known as a "loner" or "singleton" (Ferris, C. D. & F. M. Brown 1980, Butterflies of the Rocky Mountain States, University of Oklahoma Press, Norman, 442 pp.), but also has been recorded in enormous numbers and as migrating (Ferris & Brown, above; Howe, W. H. 1975, The butterflies of North America, Doubleday and Co., Garden City, New York, 633 pp.; Williams, C. B. 1930, The migration of butterflies, Biol. Monogr. & Manuals No. IX., Edinburgh, Oliver & Boyd, London, 473 pp.). The observations were made in California in July 1986. Specimens were identified by one of us (ENL).

On 25 July 1986 while driving E on US Interstate Hwy. 80 (I-80) at Pla-Vada, which is on the boundary between Placer and Nevada counties, a dense flight of *N. californica* was noted moving to the SW. This locality is 12 km E of the junction of I-80 and California State Hwy. 20 at an elevation of 1860 m. For a road distance of 400 m, butterflies swarmed over the highway in such numbers that they hit the automobile faster than they could be counted. So many insects both living and dead were in the air turbulence of automobiles that they constituted a distraction to motorists. The density of this moving population gradually decreased eastwardly for 1.5 km at which point no further butterflies were seen. The time was 1145 h (PDT), temperature was 19°C, and relative humidity 35% under clear skies. Wind was estimated to be at 10–12 kmh out of the N.

About 15 minutes later, more eastwardly on I-80, at the Donner Summit Rest Area, Nevada Co., located 12 km W of the junction of California State Hwy. 89 (S) and 24 km E of Pla-Vada, at an elevation of 2203 m, another flight of the species was observed. This migration was as dense as that noted above, and presumably was a part of the same population surge. The most dense section of this portion of the swarm stretched about 800 m along I-80. After the dense swarm was passed, lesser numbers were observed for 8 km E of Donner Pass to the Donner Lake Interchange (elevation ca. 2000 m). This second encounter with what we assume to be the same flying population observed earlier in the day was flying SW under weather conditions similar to those noted above.

At the Donner Summit Rest Area, 8 butterflies (2 ♂, 6 ♀) were collected from the dead in a windrow along the road. Dead butterflies numbered 20–50/m² of roadside area, and extended along I-80 for at least 3 km. No species other than *N. californica* were noted among the dead. While this estimate gives some idea of the large numbers killed, visual

estimates indicated that those in flight numbered 5–25 butterflies passing the migration corridor each second. The height of flight was 1–4 m above the ground. Repeated counts of this unidirectional flight gave similarly steady readings of the moving population. As judged from the abundance of dead insects compared with those passing in flight, this flight had been taking place for more than two h.

Three days later, on 28 July 1986, on a westward return trip, the migration was still in progress, but with fewer individuals spread over a longer distance. On that date, 10–25 butterflies could be counted in the air from anywhere within a circle. This flight extended from the Donner Lake Interchange over the Donner Pass through Norden, Soda Springs, and Cisco to the junction of I-80 and California State Hwy. 20, a distance of 42 km. Three specimens (2 ♂, 1 ♀) were collected at the W-bound Donner Summit Rest Area. Climatic conditions were clear skies, no wind, 18°C, and about 30% relative humidity. Migration was westward 1–9 m above the ground. All 11 voucher insects are in the Insect Collections of the Department of Entomology, Louisiana State University, Baton Rouge.

Later, on 1 August 1986, at the Donner Summit Rest Area, no individuals were seen in flight. Apparently the migrating population noted four to seven days earlier had moved through, and was no longer to be seen here.

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SPEYERIA COLLECTION OF PAUL GREY TO THE
AMERICAN MUSEUM OF NATURAL HISTORY

The incomparable collection of the genus *Speyeria* (Nymphalidae) of Paul Grey has been deposited in the American Museum of Natural History. It consists of some 19,700 mounted specimens, including 263 paratypes, with series from throughout the range of every species. The number of specimens ranges from a low of 94 for *diana* up to 4366 for *atlantis*. This material has been incorporated into the Museum's collection, which includes the Gunder and dos Passos specimens, among others, to form a study collection of 37,800 butterflies in this one genus.

In addition to the specimens, about 150 genitalic preparations were received. These were made to study and help define each species, and formed the basis for "A genitalic survey of Argynninae (Lepidoptera, Nymphalidae)" by C. F. dos Passos and L. P. Grey (1945, Am. Mus. Novitates, no. 1296, 29 pp., 54 figs.). Additional study led the same authors to their "Systematic catalogue of *Speyeria* (Lepidoptera, Nymphalidae) with designations of types and fixations of type localities" (1947, Am. Mus. Novitates, no. 1370, 30 pp.). Grey made a list of the specimens and slides used in the former paper, which is in the museum's files; not all the material studied was available in the Grey and dos Passos collections.

A catalogue on 3″ × 5″ index cards has been presented to the Museum also, listing and commenting on many of the specimens, by species and locality, that were studied by Paul Grey over the years. This takes up about two linear meters. Much valuable distributional data is included in this file; it also lists many butterflies not in his collection.

The *Speyeria* collection of the American Museum of Natural History now contains not only the primary types of about one-third of the approximately 160 available names, but paratype and topotypical material of all, or nearly all, the specific and infraspecific names. The study collection has the specimens arranged by counties within the contiguous United States, and by neighboring areas in Mexico, Canada, and Alaska. Study of the distribution and variation within each species is simplified when the butterflies are pinned out in this manner. One result of this curating is that it quickly became evident to me that the majority of the subspecific names proposed in this genus are, at best, but random points on or at the ends of various clines, and hence are of little or no scientific value. There appear to be very few completely allopatric populations to which legitimate names might be attached.

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MANUSCRIPT REVIEWERS, 1986

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BOOK REVIEWS

CALIFORNIA BUTTERFLIES, by J. S. Garth and J. W. Tilden. 1986. University of California Press, Berkeley, California. 246 pp., 20 color plates, hardcover. $19.95.

California leads the nation in lepidopterous interest according to membership in the Lepidopterists' Society. This first of two contemporary books aimed at the California audience (Emmel & Emmel will be at least another year in process) is a great disappointment. The book offers little more and a great deal less than its classic 60-year-old antecedent, Comstock's *Butterflies of California*. The rather out-of-perspective dust cover illustration is a metaphoric warning about the contents. Following on the heels of Opler and Krizek, and the just published Scott, this work falls in the category of an anachronism.

The authors introduce the book as a field guide, so that "users may learn where to find the butterflies and skippers of California . . . may learn how to observe these Lepidoptera, how to study their fascinating habits, how to record observations so they will have meaning to others, and how to collect and preserve specimens." Of these topics, the overwhelming emphasis is on collecting. With space at a premium, we here get a half page figure on how to mount a moth ball on a pin without mention of the Environmental Protection Agency listing of naphthalene as a potent carcinogen. In contrast, there are two and a half pages on disappearing butterflies. But not to despair. Even though major expansion of urban areas has led to major irreparable habitat destruction and extinctions, "freeways provide quick access to some more distant butterfly haunts." I was unable to find anything substantive on how to study habits or make meaningful observations, although these two topics should charge the goals of today's butterfly "collector."

The field guide aspect of the book is another unfilled promise. Here we are instructed to use the key to families and then thumb through the illustrations. Without dwelling on the quality of the latter, one must conclude this could be a very frustrating experience. There are no maps, only general distribution data, and limited information on flight periods. Life history data are exemplified for *Glaucopsyche lygdamus*: "egg echinoid, flattened, with a raised white network; larva bright green with a magenta dorsal band; pupa brown with black dots." This kind of "description" is unfortunately not unique to this book, but stands as a sad commentary on the primitive and almost useless state of information on early-stage morphology.

In the wisdom of recognizing that to look up information on, discuss, or exchange a specific butterfly, you need to know its name, Garth and Tilden than go on to unquestioningly apply the 1983 Miller and Brown check list (as in Check list of the Lepidoptera of America north of Mexico, R. W. Hodges, ed.). Not to add more to this over-discussed issue, it may be worth noting that the decision will hardly help those attempting to "look up" information on some of the appellations. *Occidryas editha* won't yield much from *Biological Abstracts*, although this butterfly is widely used in population studies. A further deference to instability with the use of common names is incredible: "What should become of a common name that is based on a scientific name that changes? The mountain vagabond was a perfect common name for the fritillary *Argynnis* (now *Speyeria*) *montivaga*. But because *montivaga* has been shown to be a synonym of *egleis*, its common name has been changed in the present field guide to Egleis Fritillary." Follow that logic and you might understand the charge of the Light Brigade. Failure of the authors to confront the ferment in taxonomy and nomenclature can be expected to turn off any serious users of the book, who, in consulting other resources will wonder what is going on, and why.

A brief history of butterfly collecting in California was the section I personally found most interesting—but then I have lived a good part of it. Some of the really flavorful stories, those uniquely Californian, are missing. We should have recorded such events as the night an intense midget jumped up during a Lorquin club meeting and called John Comstock a Nazi murderer for taking 500 Atossa fritillaries in a day. Then, the midget may have had a point because Atossa was never common after that day and became extinct three decades later.

I must recommend waiting and hoping Emmel and Emmel will answer our prayers. It is difficult being so negative about a work that caps two lives of involvement by two fine gentlemen who have otherwise contributed a great deal. To do otherwise would not be fair to the present generation.

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BUTTERFLIES OF EUROPE, Vol. 8, *Aspects of the Conservation of Butterflies in Europe,*
Otakar Kudrna, Ed. (and author). 1986. AULA-Verlag, Wiesbaden 1, West Germany.
323 pp. Order from: E. J. Brill, P.O. Box 9000, 2300 PA Leiden, Netherlands. $129.50
(series subscription price $111.25).

Although Vol. 8 is last in the *Butterflies of Europe* series, it is the second volume
published. The title belies the contents, which are broader than butterfly conservation.
This book consists of a Preface, 6 chapters, and a 14-page Bibliography. There is no index,
but there is a detailed table of contents. Chap. 1 is a 4-page introduction to the aims,
scope, materials, and methods related to this treatise. Chap. 2 is also short (18 pp.) and
makes a case for using native butterflies as environmental health indicator species. Several
species-specific examples are presented. There is a discussion of the order Insecta, followed
by description of the six main European biomes cited in the book.

Chap. 3 (81 pp.) treats the material of the book's title. Starting with a biogeographic
history of European butterflies during the Holocene, the author progresses to anthropo-
genic factors harmful to butterflies. The latter subject is treated in detail, and discussion
is liberally illustrated with colored photographs of habitats. Kudrna has identified 11
anthropogenic (introduced by man) and 4 natural factors that comprise the pressures on
any butterfly species. Among the former are air pollution, agricultural activities, urban-
ization, and overcollecting; among the latter, climatic conditions, parasitoids, competition,
and predators. Each factor is discussed with appropriate photographs and recognition of
sensitive species. Causes and effects are examined with suggestions for protection measures.
The author's treatment appears well balanced; he does not come across as a zealot in any
sense. A few traditional conservationists may be offended by some of Kudrna's comments,
but I believe he has researched his subject carefully and thoroughly. He has addressed
butterfly collecting in great detail from the aspects of scientific collecting, hobby collecting,
and commercial collecting. The treatment is fair and covers pros and cons equally. The
author points out the value of scientific collecting for demographic and taxonomic re-
search; that destructive effects of overcollecting are not directly comparable to the re-
percussions of habitat destruction; and that in Germany (as an example) each species
threatened by overcollecting is more seriously threatened by man-made pressures. These
pressures are usually the main cause of decline in butterfly numbers, not collecting *per
se.* He points out that rare butterflies are sought because of their rarity, and that commercial
collecting may pose a threat to some.

Kudrna is critical of "Red Data Books" and other lists of rare, threatened, or endangered
species. He presents cogent and documented arguments to support his position. He also
points out that even in Europe, where butterflies have probably been studied more
intensively than anywhere else, there are vast gaps in the knowledge of geographic
distributions of many species. He demonstrates that considerable misinformation regard-
ing geographic distributions has been promulgated from author to author. The conse-
quence is that butterflies have been listed as endangered in some areas where, in fact,
there are no valid records that they ever occurred. He calls for objectivity and use of
accurate data, rather than emotion and conjecture. This stance will be unpopular with
some readers, but it is valid and the point needs to be made. The last portion of Chap.
3 evaluates the present state of knowledge of European butterflies. Kudrna concludes that
much has yet to be learned concerning ecology, faunistics, distribution, and early stages,
a situation certainly not unique to Europe.

Chap. 4 (103 pp.) is entitled "Applied taxonomy of European butterflies". Nearly half
of this chapter is devoted to interpretation and explanation of the Code of Zoological
Nomenclature published by the International Commission on Zoological Nomenclature.
This treatment is informative and useful, but one questions its inclusion in a volume
dealing with butterfly conservation. The Code discussion is followed by a 14-page glossary
of taxonomic terms. Again the information provided is useful, but out of place. It would
be more appropriate for the yet-to-be published Vol. 2, *Introduction to Lepidopterology.*
The remainder of Chap. 4 consists of an annotated checklist of European butterflies, a
provisional synonymic checklist, and a 2-page summary of "priority tasks in taxonomic

research". Thus all of Chap. 4 would seem to belong in Vol. 2, although the chapter is certainly valuable and well presented.

Chap. 5 (69 pp.) returns to conservation and is devoted to applied biogeography of European butterflies. Following a short prefatory section, it is composed primarily of maps and tabular data. The author first defines biogeography in a broad sense, as opposed to zoogeography and faunistics. The area of concern to the author is conservation of the natural environment using butterflies as a representative animal group. Butterfly colonies across Europe are surveyed, with tabular distributional data for all species. In addition to qualitative data, Kudrna develops a Chorological Index (CI) for each nominal species based on the sum of numerical values for size, composition, and affinity of range (as defined in the text). The smaller the CI value, the more successful the species. Large CI values indicate endemic species in limited areas. Evaluations of the "health" at the species level of all European butterflies are tabulated. Health factors include population declines, habitat vulnerability, and species vulnerability. These factors are assigned numerical values, and Vulnerability Indices (VI) from 1 to 6 are calculated (6 indicating most vulnerable). The latter portion of Chap. 5, well illustrated by color photographs, discusses butterfly ecology and habitats.

The final chapter (22 pp.) outlines a comprehensive program to conserve European butterflies. Certain sensitive species are identified and discussed, and color photographs of their typical habitats included.

This book is clearly written and the author amassed and digested a formidable amount of data. He has attempted to quantify data related to biogeography and species vulnerability, thus removing much of the conjecture associated with typical conservation treatises. Data are presented, conclusions drawn, and positive recommendations are made. As indicated by numerous photographs, the author visited and studied many regions in Europe and has first-hand information.

Like its predecessor, this book is in English, is well manufactured and attractively produced. I noted a few typographical errors and lapses into German (such as *ist* for *is*). The only deficiency is the absence of a glossary of ecological terms. There is liberal use of arcane terms such as "nemoral", "eurychoric", "eurytopic", "xerothermophils", "ubiquists", etc., which will not be familiar to the general reader. Other terms appear to be literal translations of German compound words. Perhaps a glossary can be included in a future volume.

Although restricted to European species, this book belongs on the shelf of any serious lepidopterist. It contains a wealth of information and procedures. The treatment is well balanced and well researched. A serious attempt was made to quantify information. It is a scientific approach, and I suspect may well serve as a model for subsequent books on invertebrate conservation in regions other than Europe.

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Cover illustration: Semilooping larva of the strange noctuid *Phyprosopus callitrichoides* on *Smilax.* Sketch by Mark Klingler, Carnegie Museum of Natural History. Suggested by John E. Rawlins.

PATTERNS OF OVIPOSITION IN *HEMILEUCA LUCINA* (SATURNIIDAE)

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ABSTRACT. *Hemileuca lucina* (Saturniidae) is a batch-layer, ovipositing on stems of *Spiraea latifolia* (Rosaceae) in the fall, three months after larval development is completed. Eggs hatch the following spring. Patterns of oviposition and choice of oviposition site were determined by sampling three natural populations of this moth in Massachusetts. Mean number of eggs per mass was 146, with no decrease in the weight of eggs laid later relative to earlier in the mass. Females made few mistakes in choice of hostplant, and chose stems in sunny locations near the edge of *S. latifolia* clumps. Egg masses were deposited near the ground at a mean height of 33 cm, and on twigs between 1 and 5 mm diam.

Additional key words: eggs, *Spiraea latifolia*.

Choice of oviposition sites may be critical for the reproductive success of an individual insect. Although mistakes in the selection of appropriate oviposition substrates occur (Chew & Robbins 1984), generally females are discriminating in where they lay their eggs (Rausher 1979a, 1979b, Stamp 1982, Singer 1983, 1984, Williams 1983, Grossmueller & Lederhouse 1985). Appropriate choices may be particularly important for insects that lay eggs in batches, because they may make only one to a few decisions of where to oviposit. This is in contrast to species that oviposit eggs singly, where females may make hundreds of such decisions.

Most studies on oviposition behavior have dealt with species in which eggs are deposited the same season in which the larvae feed, when cues are available that indicate appropriate larval host plants and environ-

ment. For example, Rausher (1979a) demonstrated that ovipositing *Battus philenor* (L.) (Papilionidae), whose offspring feed in that same season, discriminate among host plants and benefit by choosing plants that will not senesce before the larval period ends. Williams (1981) found that ovipositing *Euphydryas gillettii* Barnes (Nymphalidae) butterflies chose leaves of the host plant with an orientation towards the sun that minimized larval development time, a critical component of larval survival in the montane habitats with short growing seasons where these butterflies occur. In contrast, cues such as hostplant quality and microclimate, which are directly related to offspring survivorship, may not be available to species that deposit eggs in the growth season prior to that in which larvae feed. Some of these species deposit eggs a few weeks after the larval period [gypsy moth, *Lymantria dispar* (L.) (Lymantriidae), and tent caterpillars, *Malacosoma americana* (Fab.) and *M. disstria* (Hübn.) (Lasiocampidae)], whereas others oviposit months after the larval period (species of tribe Hemileucini in Saturniidae) (Ferguson 1971, Tuskes 1984).

Our objective was to examine oviposition behavior and site selection of *Hemileuca lucina* Hy. Edw. (Saturniidae), an insect that lays batches of eggs three months after the larval period and in the growth season before that in which larvae feed.

Like other hemileucines, *H. lucina* is univoltine. The flight period occurs in mid to late September and lasts about two weeks. Females eclose laden with eggs. They attract males by producing a pheromone, apparently as soon as their wings expand, as Tuskes (1984) noted for other hemileucines. In the laboratory (at about 22°C), copulation lasts 1 to 2 h ($\bar{x}$ = 92 min ± 50 SD, n = 13). Females begin depositing eggs shortly afterwards.

Females deposit usually 1, but occasionally 2 (less than 5% deposit 2), clusters of eggs in a ring around stems of the host plant, *Spiraea latifolia* (Ait.) Borkh. (Rosaceae) (Fig. 1). The female climbs onto a twig and curls the abdomen up and to the side around the twig for each egg deposited. She alternates from side to side, with two depositions made swinging the abdomen to the left and then two to the right. The first few eggs are laid in a sparse half-circle around the twig. The female then works her way up the twig, carefully inserting eggs into the gaps among the others, thus making a tightly packed egg ring. Usually, several rows are deposited, with the rows progressing up the stem.

The eggs overwinter and, in Massachusetts, hatch sometime in May, depending on local weather conditions. Larvae are gregarious in the first four instars. Group size declines, and by the fourth or fifth instars solitary individuals are observed in the field (Cornell et al. 1987). Factors such as parasitoids and predators, weather, and food availability con-

FIG. 1. Egg mass of *H. lucina*. Top, longitudinal view. Bottom, stem of *Spiraea latifolia* cut to show arrangement of eggs around it.

tribute to reduction in group size. Larvae are black with spines in the first five instars. The spines cause painful dermatitis when larvae are handled, particularly in the penultimate and ultimate instars. Larvae are solitary in the sixth instar and usually have a lateral yellow stripe

and yellow mottling, but can be quite variable (D. F. Schweitzer pers. comm.). Although larval feeding in the early instars is confined to *S. latifolia*, we observed that later instars may feed on other plants, such as blackberry (*Rubus* sp.), cinquefoil (*Potentilla* sp.) and black cherry, *Prunus serotina* (Rosaceae). The larvae leave the host plant, often move some distance, and burrow into the soil to pupate, where they aestivate through the rest of the summer.

Materials and Methods

Egg masses were collected from Dover, Norfolk Co., Massachusetts, in 1983 and 1984; Belmont, Norfolk Co., Massachusetts, in 1984; and Leverett, Franklin Co., Massachusetts, in 1984 and 1985. Number of eggs per mass was counted at these 3 sites. In 1985, we determined the percent of eggs hatching at Leverett.

To examine whether the first eggs deposited weighed more than those deposited later, as has been found in other lepidopterans (Wellington 1965, Leonard 1974, Richards & Myers 1980, Jones et al. 1982, Wiklund & Persson 1983, Karlsson & Wiklund 1984, Harvey 1985), eggs from newly laid egg masses were detached from twigs and weighed individually. Because we were unable to determine the exact order of deposition but knew that eggs were laid from the bottom to the top, we removed nine eggs from the bottom ring and nine from the top ring of each of five egg masses. The null hypothesis was that no difference in egg weight occurred between eggs laid first and those laid last.

At Leverett in 1984 and 1985, we described the location of egg masses. We first measured the height at which they occurred on *S. latifolia* stems. On 19 May 1985, we measured, to the nearest 10 cm, their distance from the edge of *S. latifolia* clones. In addition, we noted whether masses were located in the sun or shade. We also searched outside dense clones of *S. latifolia* for egg masses.

To determine what diameter of stem females selected for oviposition, and whether that reflected what was available, we compared diameter of stems containing egg masses with that of stems that were available. On 14 April 1985, the diameter of available stems was measured by establishing transects through clones of *S. latifolia* at Leverett. A transect was set up through the middle of each of two clones, and another transect along the edge of these same clones, for a total of four transects. The height used for sampling diameter of available stems was based on mean height above ground of egg masses the previous year (1984) at that site ($\bar{x}$ = 24.9 cm ± 11.4 SD, n = 33). Every stem within 5 cm of the transect was measured at a height of 25 cm. We assumed that relative availability of stems of different diameters did not change

TABLE 1. Number of eggs in egg masses of *Hemileuca lucina* from three sites in Massachusetts. Dover "a" refers to egg masses collected in 1983, hatching that year, and Dover "b" refers to egg mass remains collected in 1984, hatching in 1983.

Location	Year	Mean ± SD	n
Dover	1983a	156.4 ± 44.1	17
	b	142.1 ± 43.9	53
	1984	135.2 ± 44.5	34
Belmont	1982	157.4 ± 39.1	5
	1983	121.0 ± 19.8	2
Leverett	1983	147.4 ± 50.8	32
	1984	149.9 ± 47.8	33
Total		145.8 ± 44.7	176

during the study. New stems are produced each year, old ones grow, and there are thousands of stems available from which females may choose.

Power of the statistical tests (probability of not committing a type II error, $1 - \beta$) was calculated as described by Cohen (1977).

RESULTS AND DISCUSSION

Description of the egg mass. A typical egg mass is shown in Fig. 1. Mean weight of an egg from a single mass was 1.63 mg ± 0.16 SD and ranged from 1.13 to 1.89 mg (n = 118). Such variation in egg weight may or may not relate to larval fitness (Wellington 1965, Richards & Myers 1980, Wiklund & Karlsson 1984, Karlsson & Wiklund 1984, Harvey 1985). In general, weight of eggs when laid declines as lepidopteran females age (Wellington 1965, Leonard 1974, Richards & Myers 1980, Jones et al. 1982, Wiklund & Persson 1983, Karlsson & Wiklund 1984, Harvey 1977, 1985, Boggs 1986). Accordingly, for those species laying only one or two egg masses, egg weight would be predicted to decline from first to last eggs laid in a single mass, as Wellington (1965) found for *Malacosoma californicum pluviale* (Dyar) (Lasiocampidae). However, we found that the first eggs deposited in an *H. lucina* egg mass were not significantly different in weight from eggs deposited last (Wilcoxon paired sample test, n = 5, P > 0.05). Because *H. lucina* females do not feed as adults, often mate and oviposit within a few hours of eclosion, and usually lay only a single egg mass, they may emerge with all eggs yolked and allocate resources to eggs randomly (Wiklund & Karlsson 1984).

The mean number of eggs per mass was 145.8 (Table 1), and ranged from 42 to 235. Of 36 egg masses collected in Leverett in 1984, 2 did not hatch; of 33 egg masses collected there in 1985, again 2 failed to hatch. Even within an egg mass, not all eggs hatched. Of the 31 egg

NUMBER OF EGG MASSES
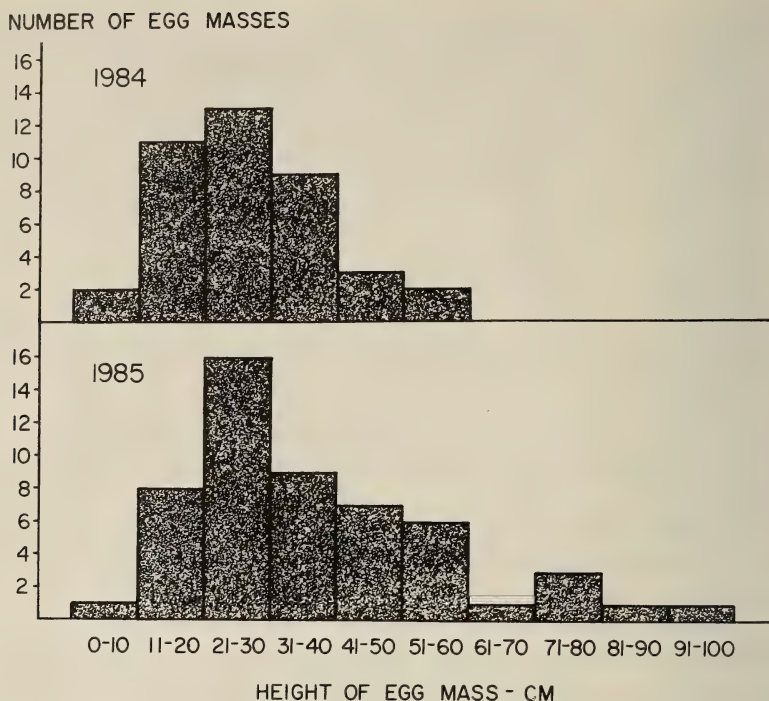
FIG. 2.   Distribution of above-ground height of *Hemileuca lucina* egg masses in 1984 (n = 40) and 1985 (n = 53) at Leverett.

masses from Leverett that hatched in 1985, a mean of 12.9% (±16.5 SD, range 1.1–93.5%) of eggs per mass did not hatch.

Location of egg masses. Females were quite specific about where they laid eggs. Of 38 egg masses at Leverett in 1985, only 2 were on nonhost plants, 1 on blackberry (*Rubus* sp., Rosaceae), and 1 on gold-enrod (*Solidago* sp., Asteraceae). Both "mistakes" were located in the midst of dense clumps of *Spiraea latifolia*, and probably did not ad-versely affect larval survival. Newly hatched larvae may move more than 100 cm to find food. Mean height of egg masses at Leverett was 32.8 cm (±17.3 SD, n = 93) (Fig. 2). Height distribution of masses did not differ significantly between 1984 and 1985 (χ^2, df = 6, P > 0.10, $1 - \beta = 0.55$, $\alpha = 0.05$). Stem height of *S. latifolia* ranged up to about 200 cm; thus, females were avoiding the higher sites. Eighty-five percent of the masses occurred below 50 cm (Fig. 2).

Females chose stems of a particular diameter (Fig. 3). Egg masses occurred on stems between 1 and 5 mm diam., whereas the available stems ranged from less than 1 mm to 12 mm. The size categories of
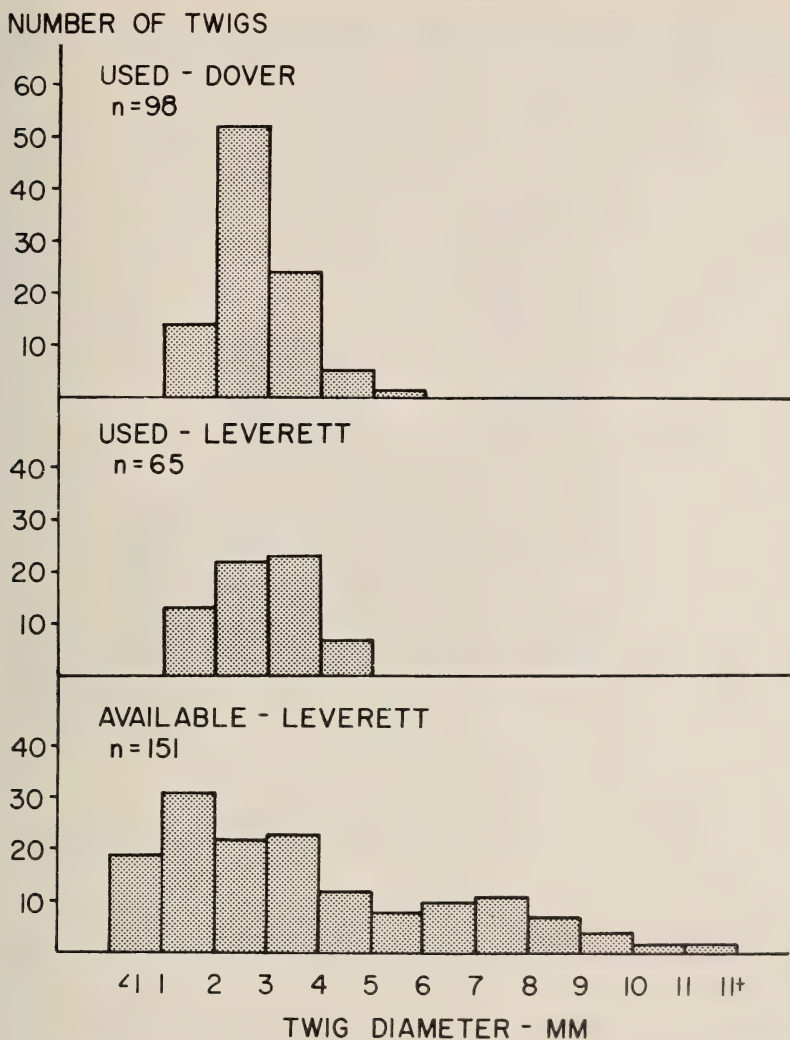
FIG. 3. Diameter of stems at height of 25 cm available to ovipositing *Hemileuca lucina* females compared to diameter of stems chosen for oviposition.

stems used and those of available stems at Leverett were significantly different (χ^2, df = 4, P < 0.001) (Fig. 3). Diameter of stems chosen by females at Leverett and Dover were not significantly different (χ^2, df = 4, P > 0.05, 1 − β = 0.57, α = 0.05) (Fig. 3).

All egg masses occurred in portions of *S. latifolia* clones not shaded by trees or shrubs during the day (n = 38, Leverett 1985). Thus, females appeared to avoid shady locations. In addition, females chose oviposition

PER CENT OF EGG MASSES

DISTANCE OF EGG MASS
FROM EDGE OF CLONE (cm)

periphery ⟶ interior
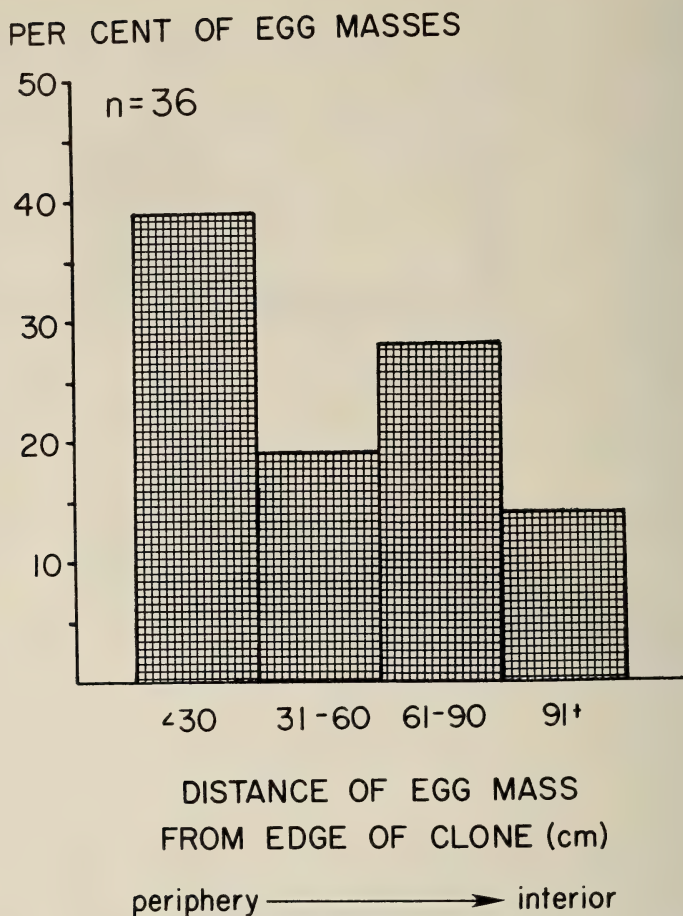
FIG. 4.   Distribution of egg mass position in clones of *Spiraea latifolia* at Leverett in 1985.

sites on the periphery (0–60 cm) of *S. latifolia* clumps (Fig. 4), where more sunlight was available.

Our results show that *H. lucina* females chose stems of *S. latifolia* that were a specific subset of those available for oviposition. First, such stems were located near the periphery of a clump and in the sun. This may aid in synchronizing egg hatch with bud burst, which is important in other species (Feeny 1970, Williams 1981). Second, egg masses were low on the stem, which may keep at least some under snow during the winter and ensure a more even microclimate. However, mean maximal monthly snow depth was 21.7 cm (±20.7 SD; n = 102 months, 1971–80 for 2 sites, Blue Hill Observatory near Dover, and Worcester, Mas-

sachusetts; National Climatic Center 1971–80). That suggests that most egg masses (mean height 32.8 cm above ground) were seldom covered by snow. Third, females chose stems of a particular diameter. If stems are too small, the eggs may not fit together to make a tight ring, and if they are too large, too few rows may be deposited to secure the ring to the stem. Finally, mistakes in choice of hostplant species were rare and usually occurred in the midst of *S. latifolia* clumps, suggesting that females may be attracted visually or olfactorily to the host plant, and that contact with chemical cues from the stem is less important.

Ovipositing females of other lepidopterans are reported to discriminate successfully among hostplant species (Chew & Robbins 1984), seek sunny locations (Williams 1981, Grossmueller & Lederhouse 1985), choose microhabitats where desiccation problems are lessened (Carroll et al. 1979), and confront physical constraints posed by host plants (Levin 1973). Female *H. lucina* exhibit all of these levels of discrimination, even though they oviposit at a time when conditions may be different from those when larvae are feeding.

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PREDATION BY *ANOLIS* LIZARDS ON *BATTUS PHILENOR* RAISES QUESTIONS ABOUT BUTTERFLY MIMICRY SYSTEMS

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ABSTRACT.   *Anolis* lizards in Texas make supposedly distasteful and poisonous *Battus philenor* adults a component of their natural diet. The lizards appear to suffer no ill effects, and individual lizards will eat *Battus* more than once. We followed individual female butterflies searching for oviposition sites for 90 h and observed 4 instances of predation in the field. We supplemented these observations with field experiments and a laboratory study. Results raise questions about the general importance of lizard predation in the evolution of butterfly mimicry systems.

Additional key words: Papilionidae, aristolochic acid, distasteful butterflies, pipevine swallowtail.

Mimicry is widespread in nature, and studies of predation on butterflies have been prominent in the development of ideas about aposematic coloration (Brower 1958, Brower et al. 1963, Rothschild et al. 1972). Most of these studies have involved examining the behavior of captive predators when offered palatable and distasteful butterflies. There is remarkably little information on predation of adult butterflies in nature, and published field observations deal almost exclusively with attacks of birds on butterflies (Fryer 1913, Rutowski 1978, Wourms & Wasserman 1985). Observations of natural predation by lizards are rare (Ehrlich & Ehrlich, 1982), yet "birds and lizards have long been considered to be the major selective agents responsible for the extreme diversity of unpalatable and mimetic forms of butterflies in nature" (Boyden 1976). When wild *Ameiva* lizards in their natural habitat were fed live butterflies, they quickly became conditioned to avoid unpalatable species (Boyden 1976). Ehrlich and Ehrlich (1982) observed iguanid lizards preying on tropical butterflies, and because different butterfly species seemed to be attacked differently, concluded that their observations supported the assumption that lizards are often strong selective agents in the evolution of butterfly color patterns and behavior.

One classic study of mimicry in butterflies focused on the pipevine swallowtail and its mimics. The larvae feed on plants in the genus *Aristolochia* (Aristolochiaceae). The adults are distasteful to birds (Brower 1958), presumably because they sequester distasteful aristolochic acids and related alkaloids, as do other *Aristolochia*-feeding papilionids (Euwe et al. 1968, Rothschild et al. 1972). These substances are poisonous to

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generalist insects in small quantities (Rausher 1979) and in vertebrates can cause acute renal failure (Hedwall 1961, Jackson et al. 1964). Mimetic species include *Papilio troilus*, dark-form *P. glaucus* females, *P. polyxenes*, and *Limenitis archippus archippus*.

During a field study of *Battus philenor* in the John Henry Kirby State Forest, Tyler Co., Texas, we observed individual females searching for oviposition sites for a total of 90 h from 22 March to 9 May 1985. We observed four instances of predation on *Battus* by lizards, as well as two unsuccessful attempts. These observations and additional experiments cause us to question whether qualities that render butterflies distasteful to birds also render them distasteful to lizards.

Instances of Predation

Our first observation of lizard predation involved an aging *Battus* female that alighted on a host plant and started to deposit eggs. Within seconds of alighting, a large *Anolis* pounced on her from a tree trunk about 0.4 m away, apparently killing her with its first bite, which covered her head and thorax. The lizard consumed the entire butterfly during the next 20 minutes. Getting the wings into its mouth appeared to be the most difficult part; it had to scrape the butterfly many times against a tree trunk using sideways movements of the head to work the wings in. Three other similar instances were also observed. Afterwards, we collected these lizards, and they exhibited no ill effects during 24 h in captivity.

In one case, a basking butterfly escaped when an *Anolis* pounced on it. Another time, a medium-sized *Anolis* jumped from a thin branch onto a stationary copulating pair on a twig about 30 cm below it, collided with them, dislodged the male, and fell about 2 m into the undergrowth below. Before its jump, the lizard was observed to climb slowly from near the pair up to the launching point. Apparently *Anolis* can perceive motionless *Battus philenor*.

Reaction of *Anolis* to Offered Butterflies

Tethered butterflies were presented to *Anolis* in the field. One female and five male *Battus* were allowed to fly past large (>15 cm) perching lizards. In all but one case in which the lizard appeared to be startled by the observer, the butterflies were seized immediately, sometimes by the body, and sometimes by the wings. The bodies but not the wings were eaten because tethers prevented lizards from freely scraping the wings against tree trunks.

Two medium-sized (10–15 cm) lizards were each offered a *Battus* male. One lizard made no attempt to capture it. The second seized the butterfly immediately, but the tether became entangled in a twig; the lizard could not bring the dead butterfly to the ground and eventually abandoned it. We broke the wings of another butterfly near their base, making it unable to fly, and presented it to a large lizard perched on a tree trunk. The lizard immediately seized and consumed it entirely.

Three small (<10 cm) lizards showed no interest in butterflies offered to them. They are almost certainly not large enough to capture and hold a *Battus* even if they tried. None of the lizards that ate butterflies exhibited any adverse symptoms during 24 h in captivity.

Effect of Experience on Subsequent Predation

Clearly, large *Anolis* lizards often kill and eat *Battus philenor* butterflies. It is possible that the predation we observed involved lizards that had not previously consumed a *Battus* adult. The question therefore remained whether eating one would discourage a

lizard from doing so again. To answer this question, we captured two large *Anolis*, placed them in a cage and fed both a *Battus* male the first day, a female the second day, and a male on each of the following two days. The lizards caught all butterflies immediately. Usually, the entire butterfly was consumed. We conclude that either *Anolis* lizards do not learn from experience to avoid *Battus* or the butterflies are not poisonous or distasteful to them.

Discussion

Our observations indicate that *Anolis* lizards readily attack and consume an insect that serves as a model in a large mimicry complex. Qualities that render *Battus* distasteful to birds (Brower 1958) apparently do not render them so to *Anolis*. If this conclusion is applicable to other types of lizards, then lizard predation may have served less often than generally assumed as a major selection pressure causing the evolution of unpalatability or of mimicry.

Three caveats must be added to this suggestion. First, because *B. philenor* is abundant in E Texas, it may constitute a potentially abundant resource for *Anolis*. It is thus plausible that these lizards have evolved to tolerate or detoxify the noxious compounds sequestered by *B. philenor*, and thus may not be representative of all lizards. Second, it is possible that in the year of our study alternative food resources for *Anolis* were scarce, and the lizards preyed on *Battus* despite distastefulness and possible subtle adverse effects. If so, then when alternative resources are more abundant, *Anolis* may exhibit less tendency to consume *Battus*. In such years the distasteful individuals would be protected from lizard predation. This protection would favor the evolution of distastefulness and mimicry. Third, *B. philenor* in E Texas may not be distasteful, perhaps because it does not sequester noxious compounds. Two lines of evidence argue against this hypothesis: both butterflies and host plants contain aristolochic acids (Rausher unpubl. data); and female *Papilio glaucus* occur there predominantly in the black form, indicating that Batesian mimicry there is effective, which implies that *Battus* there is distasteful.

Despite the caveats, we believe our observations suggest that lizards in our study have not been a major selective force in the evolution of mimicry and distastefulness in *Battus philenor*. Our results contrast sharply with those of Boyden (1976), indicating that the influence of lizard predation on the evolution of mimicry systems needs more investigation.

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NEW RECORDS OF BUTTERFLIES
FROM THE WEST INDIES

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ABSTRACT. In 33 person-days in the field, 503 specimens of butterflies were collected in the Cayman Islands and northern Lesser Antilles. Twenty-two species are reported for the first time from the islands of Anguilla, St.-Martin, St.-Barthélémy, Saba, St. Eustatius, and Nevis in the latter group (41 individual island records). Four species are reported for the first time from the Cayman Islands, as well as five new island records, bringing the number known from these islands to 44.

Additional key words: distribution, Cayman Islands, Lesser Antilles.

This paper deals with the Cayman Islands and the northern Lesser Antilles. It is based on two recent collections. Henderson collected on seven northern Lesser Antillean islands during 29 January–20 February 1987 (23 person-days), visiting Anguilla, St.-Martin, St.-Barthélémy, Saba, St. Eustatius, St. Christopher (St. Kitts), and Nevis. Her butterflies, now in the collections of Schwartz (AS) and Gonzalez (FLG), consist of 230 specimens. A visit during 27 November–1 December 1985 (10 person-days) to the Cayman Islands by Schwartz and Gonzalez resulted in 273 specimens. Voucher specimens of some species are in the Milwaukee Public Museum. Nomenclature selectively follows Riley (1975), Miller and Brown (1981), and Brown and Heineman (1972).

CAYMAN ISLANDS

Gonzalez and Schwartz collected primarily on Grand Cayman, and Gonzalez spent one day on Cayman Brac; we did not visit Little Cayman. Previous major contributions to knowledge of the Caymanian rhopaloceran fauna are Carpenter and Lewis (1943) and Askew (1980). Table 1 summarizes present knowledge of the fauna. Of the 44 Caymanian species, 19 are now known from all three islands. Most species (41) are known from Grand Cayman (14 from only that island), with 26 from Cayman Brac and 23 from Little Cayman. Inclusion of *Her-*

aclides machaonides (Esper) (Papilionidae) rests on D'Abrera (1981: 32). But Carpenter and Lewis's comprehensive work is based on the same collection, and they did not mention such an important record. Because the situation is anomalous, we do not include this species in the numbers on the Cayman Islands. Following are supplementary notes on the species new to these islands.

Urbanus dorantes cramptoni Comstock (Hesperiidae). We collected 10 specimens (9 AS, 1 FLG) on Grand Cayman, a first report. Our series was secured at three widely separated localities (Boatswain Bay, Cayman Kai, Old Man Bay); the broad distribution of this skipper on Grand Cayman suggests that it is not an extremely recent adventive, although it must have arrived since Askew (1980) collected there in 1975.

Eurema elathea Cramer (Pieridae). This small-bodied species was recorded by Carpenter and Lewis (1943:377), and Askew (1980:128); both reported it only from Grand Cayman. Our four specimens (AS) from Cayman Brac are the first reported from that island; they were taken at the airport on the W end of the island.

E. daira palmira (Poey) (Pieridae). First reported from Little Cayman and Cayman Brac by Askew (1980:129). Our 6 specimens (5 AS, 1 FLG) are from 4 localities on Grand Cayman (George Town, Cayman Kai, Old Man Bay, Boatswain Bay).

Phoebis agarithe antillia Brown (Pieridae). "Authoritatively reported" but uncollected or unseen by Carpenter and Lewis (1943:372); record questioned by Askew (1980:131). We have 4 specimens from Grand Cayman (Boatswain Bay; 3 AS, 1 FLG) and 1 from Cayman Brac (airport, W end; AS).

Strymon martialis (Herrich-Schäffer) (Lycaenidae). Reported by both previous parties only from Little Cayman. We have 2 specimens (1 AS, 1 FLG) from Grand Cayman (Boatswain Bay) that constitute the first record for that island.

S. columella cybirus (Hewitson) (Lycaenidae). Askew (1980:127) reported this hairstreak from Grand Cayman and Little Cayman. Gonzalez collected 2 specimens (1 AS, 1 FLG) on Cayman Brac (airport, W end; Jennifer Bay), which constitute the first record for that island.

Electrostrymon a. angelia (Hewitson) (Lycaenidae). First record for this species from the Cayman Islands. A single male (AS) collected.

Hemiargus ceraunus filenus (Poey) (Lycaenidae). Known from Grand Cayman and Little Cayman (Carpenter & Lewis 1943:392; Askew 1980:128). Gonzalez took a single specimen (AS) on Cayman Brac (airport, W end).

Junonia genoveva zonalis Felder & Felder (Nymphalidae). As on Jamaica (Turner & Parnell 1985), there are two species of *Junonia* on the Cayman Islands: *J. genoveva* and *J. evarete*. We took both on Grand Cayman (Boatswain Bay; 5 AS), but only *J. g. zonalis* on Cayman Brac (airport, W end; 1 AS, 1 FLG). On Grand Cayman, interspecific contacts were of common occurrence. The two species are readily distinguished on the wing, both by phenotype and behavior; *J. evarete* is more easily approached and captured.

J. evarete (Cramer) (Nymphalidae). Widespread on Grand Cayman (George Town, Cayman Kai, Old Man Bay, Boatswain Bay; 8 AS, 3 FLG).

Anaea cubana (Druce). First record of this cuban species from the Cayman Islands (Grand Cayman). We took 16 specimens (10 AS, 6 FLG) at 2 localities (George Town, Boatswain Bay).

LESSER ANTILLES

Butterflies of individual Lesser Antillean islands were studied in the late 19th and early 20th centuries. Godman and Salvin (1884, 1896) and Hall (1936) reported on the butterflies of Dominica, St. Vincent and Grenada, and St. Christopher. Later, Pearce (1969) and Schwartz

TABLE 1. Known distribution of the 46 taxa (44 species) of Rhopalocera on the Cayman Islands.

Taxon	Distribution		
	Grand Cayman	Little Cayman	Cayman Brac
Phocides pigmalion batabano		X	
Urbanus proteus domingo	X		X
U. dorantes cramptoni	X		
Cymaenes t. tripunctus	X		X
Hylephila p. phylea	X		X
Calpodes ethlius	X		
Panoquina p. panoquinoides	X	X	X
P. sylvicola	X		
Battus polydamas cubensis	X		
Heraclides aristodemus temenes		X	
H. a. tailori	X		
H. andraemon andraemon		X	X
H. machaonides	X		
Ascia monuste eubotea	X	X	X
Appias drusilla poeyi	X	X	X
Nathalis iole		X	
Eurema elathea	X		X
E. daira palmira	X	X	X
Pyrisitia messalina	X		
P. lisa euterpe	X	X	X
Abaeis nicippe	X	X	X
Phoebis s. sennae	X	X	X
P. agarithe antillia	X		X
Aphrissa neleis	X		
Strymon martialis	X	X	
S. acis casasi		X	X
S. a. gossei	X		
S. columella cybirus	X	X	X
Electrostrymon a. angelia	X		
Hemiargus ammon erembis	X	X	X
H. ceraunus filenus	X	X	X
Leptotes cassius theonus	X	X	X
Brephidium isophthalma thompsoni	X		
Agraulis vanillae insularis	X	X	X
Dryas iulia	X		
Heliconius charitonius	X	X	X
Junonia genoveva zonalis	X	X	X
J. evarete	X		
Anartia jatrophae jamaicensis	X		X
Siproeta stelenes insularis	X		
Phyciodes phaon	X		
Euptoieta hegesia	X	X	X
Anaea cubana	X		
A. verticordia danieliana	X	X	X
Danaus plexippus megalippe	X		X
D. gilippus berenice	X	X	X
D. eresimus tethys	X		
Total	41	23	26

and Jimenez (1982) surveyed the butterflies of Barbados and Montserrat, respectively.

The only comprehensive work on the Lesser Antillean butterflies is that of Pinchon and Enrico (1969), the major source of Riley's (1975) Lesser Antillean records. All distributions below are from these two sources. Henderson collected on most of the northern Lesser Antilles. Collection notes on selected species follow.

Epargyreus z. zestos (Geyer) (Hesperiidae). Known from inner (St. Christopher) and outer (St.-Martin) chain islands and throughout the remainder of the Lesser Antilles to Grenada. One specimen (AS) taken on Saba, N of St. Christopher.

Polygonus leo savigny (Latreille) (Hesperiidae). Previously known only from the northern islands of St. Christopher and Montserrat. Collected on St.-Barthélémy (2 FLG, 2 AS). This is not only a northern extension in known range and a new island record, but the first record for the outer chain.

Urbanus proteus domingo (Scudder) (Hesperiidae). Widespread from Saba to Grenada. Not previously reported from St. Eustatius (1 AS), Nevis (1 FLG, 1 AS), or St.-Barthélémy (1 FLG, 1 AS).

U. obscurus (Hewitson) (Hesperiidae). Widespread from Saba and Antigua S to Grenada and Barbados. Not previously reported from Nevis, whence we have 2 specimens (1 FLG, 1 AS).

Pyrgus oileus (Linnaeus) (Hesperiidae). Three specimens (1 FLG, 2 AS) from Nevis fill in the previous gap between St. Christopher in the north and Montserrat in the south.

Wallengrenia ophites (Mabille) (Hesperiidae). Reported throughout the Lesser Antilles, from St.-Martin and St.-Barthélémy to St. Vincent. New records are St. Eustatius (1 AS), which lies between Saba and St. Christopher, and Nevis (1 AS) S of St. Christopher, whence *W. ophites* was known.

Hylephila phylea phylea (Drury) (Hesperiidae). Widely distributed from St.-Martin and St.-Barthélémy to Grenada and Barbados; not previously reported from St. Eustatius (1 AS) or Saba (1 AS) N of St. Christopher, the northernmost inner-chain island whence *H. p. phylea* has been reported.

Ascia monuste virginia (Godart) (Pieridae). Ranging from St.-Martin and Saba in the north to St. Lucia in the south. Previously unreported from Anguilla (1 FLG, 2 AS), St. Eustatius (2 FLG, 2 AS), and Nevis (1 AS).

Pyrisitia lisa euterpe (Ménétriés) (Pieridae). Widespread from St. Christopher and St.-Martin in the north to St. Lucia and Barbados in the south. Not reported from Anguilla (2 FLG, 2 AS), Saba (2 FLG, 2 AS), St. Eustatius (2 FLG, 2 AS) or Nevis (1 FLG, 2 AS). The first two islands are northern extensions in known range within both chains.

Eurema elathea (Cramer) (Pieridae). Broadly distributed from St.-Martin and St. Christopher to St. Lucia and Barbados. Not previously reported from Anguilla (3 FLG, 3 AS) N of St.-Martin.

Phoebis s. sennae (Linnaeus) (Pieridae). Although broadly distributed throughout the West Indies, including the Lesser Antilles, where it has been reported from St.-Martin and Saba in the north to Grenada and Barbados in the south, there are no published records for Anguilla (1 AS), to the N of St.-Martin. In the inner chain, we have specimens from St. Eustatius (1 AS) and Nevis (2 FLG, 1 AS), which fill the previous gap between Saba and Montserrat.

P. trite watsoni Brown (Pieridae). The only island known to harbor this species in the north is St. Christopher; on the more southern islands, it has been reported on Montserrat, Guadeloupe, Dominica, and St. Lucia. A single individual (AS) from Saba extends the known range from St. Christopher to the northernmost of the inner-chain islands.

Strymon bubastus ponce Comstock & Huntington (Lycaenidae). Reported from St.-Barthélémy and St. Christopher in the north to Grenada in the south. Its range extends as far N as Saba, whence we have 1 specimen (AS), and Anguilla, where Henderson took 6 (3 FLG, 3 AS).

Electrostrymon angerona (Godman & Salvin) (Lycaenidae). Occurs only on the inner-chain islands, from St. Christopher to Grenada. We have 1 specimen (AS) from Saba, thus "completing" its distribution on these northern islands.

Leptotes cassius chadwicki Comstock & Huntington (Lycaenidae). Widely distributed as far S as Grenada, records fill in the northern gaps in both the inner (Saba [5 FLG, 8 AS], St. Eustatius [2 FLG, 4 AS], Nevis [1 FLG, 1 AS]) and outer (Anguilla [2 FLG, 3 AS]) chains.

Hemiargus thomasi woodruffi Comstock & Huntington (Lycaenidae). Previously known only from four Lesser Antillean islands, as well as Désirade. A single specimen (AS) from Nevis is a new island record, S of all other northern Lesser Antillean records.

Agraulis vanillae insularis Maynard (Heliconiidae). Although known from four outer-chain northern islands, reported only from St. Christopher in the inner chain. We have specimens from Saba (2 FLG, 2 AS) and St. Eustatius (2 FLG, 2 AS) confirming its occurrence on the northernmost of the inner-chain islands.

Junonia genoveva michaelesi Munroe (Nymphalidae). Widespread but unreported from Saba (1 FLG, 2 AS), St. Eustatius (1 AS), and Nevis (1 FLG, 1 AS) from the inner chain, and Anguilla (1 FLG, 2 AS) from the outer chain.

Anartia j. jatrophae (Johansson) (Nymphalidae). Widely distributed as far S as Grenada and Barbados, but unreported from Nevis (2 FLG, 2 AS). Remarkably, Henderson did not see this species on any other island, although it was moderately abundant on Nevis. Known only from Antigua in the outer-chain islands.

Biblis h. hyperia (Cramer) (Nymphalidae). In the northern islands, known only from St. Eustatius (where Henderson found it abundant on The Quill) and St. Christopher; Henderson took one specimen (AS) on Saba.

Antillea p. pelops (Drury) (Nymphalidae). Reported only from St. Christopher and Montserrat. We have one specimen from Nevis (AS), between the foregoing islands.

Anaea minor Hall (Apaturidae). Described from St. Christopher, reported from Antigua and Montserrat, as well as Guadeloupe. A specimen from Nevis (AS) fills in the gap between Montserrat and St. Christopher. Although Pinchon and Enrico (1969) reported these leaf butterflies from St.-Barthélémy, they stated that the population there tended toward the larger Puerto Rican *A. borinquenalis* Johnson & Comstock.

Although the above island records add no new species to the 74 (95 taxa) generally accepted from the Lesser Antilles, they add information on the distribution of 22 species on the northern Lesser Antilles.

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A NEW SPECIES OF *GRETCHENA* (TORTRICIDAE) INJURIOUS TO PLANTED NEOTROPICAL WALNUT

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ABSTRACT. *Gretchena garai* is described from four males and three females reared from shoots of *Juglans neotropica* Diels. (Juglandaceae) near Loja, Ecuador. Adults differ from all known congeners by their greenish vestiture and by absence of setae on the anal extensions of male cuculli. This is the first report of *Gretchena* from continental South America and the Neotropics.

Additional key words: Olethreutinae, Eucosmini, *Juglans neotropica,* Ecuador.

I describe this new species now because of its economic importance. It was discovered injuring leader shoots of Neotropical walnut, *Juglans neotropica* Diels., in Ecuador. One- to four-year-old plantings have been attacked repeatedly in the Loja Province highlands. Injured trees develop multiple leaders which lessen their chances of producing commercial timber. Walnut is important in Ecuadorian forestry, yielding timber similar in properties and value to North American black walnut, *J. nigra* L. Several species of *Juglans,* locally known as nogal, occur naturally from S Mexico through Central America and the cordilleras of Columbia, Ecuador, and Peru to Argentina (Chudnoff 1984).

Gretchena, a genus of Eucosmini, currently comprises 11 Nearctic species, including the pecan bud moth, *G. bolliana* (Slingerland), and *G. concitatricana* (Heinrich), a black walnut shoot moth (Blanchard & Knudson 1983, Brown 1982; Naughton 1970, Powell 1983). Except for *G. watchungana* (Kearfott), whose larvae feed on *Alnus* (Betulaceae), the previously known larvae of *Gretchena,* numbering four species, feed on Juglandaceae (Miller 1987, Naughton 1970). *Gretchena* has not previously been reported from continental South America or the Neotropics (Powell & Razowski in press).

I deemed the Ecuadorian *Gretchena* to be new after comparing specimens with descriptions of all check-list species of generically unplaced Eucosmini (Powell & Razowski in press). In the description below, character states that place the species in *Gretchena* (Brown 1982) are italicized.

Gretchena garai, new species
(Figs. 1–3)

Male. Forewing 7.0–7.5 mm long (4n). **Head.** Length of second labial palpus segment 1⅙ eye diameter, whitish except for brownish black near base, middle, and apex; third segment ⅓ length of second. Face white, vertex yellowish. **Thorax.** Whitish, tegula white, brown, and green. Forewing termen concave, *costal fold extending from base to middle*

FIGS. 1–3. *Gretchena garai.* **1,** Wings of holotype female; **2,** Male genitalia (prep. WEM 2110862); **3,** Female genitalia (prep. WEM 211086).

and enclosing a white hair pencil, upper side patterned as in Fig. 1, *basal patch more distinct on inner margin than on costa,* geminations on costa white, darkest appearing areas brownish black, the less dark green, underside brownish gray, fringe brownish black. Hindwing upper and undersides, including fringe, brownish gray. **Abdomen.** Brownish gray. **Genitalia** (Fig. 2) (4n): *Uncus absent; socii separate,* bent dorsally just beyond middle; aedeagus ¾ as long as valva, *supported by long juxtal caulis,* beaked at apex, vesica with 20–30 tightly packed cornuti ½ as long as aedeagus; *valval neck sparsely spined, cucullus drawn out at lower anal margin to a spinelike tip,* this extension lacking setae even at tip.

Female. Forewing 6.0–6.5 mm long (3n). Exteriorly as described for male. **Genitalia** (Fig. 3) (3n): *Posterior margin of seventh sternum inflected, overlapping ostium bursae,* posterior corners not elaborated; eighth tergum lacking scales; *middle ⅓ of ductus bursae sclerotized,* the sclerotization encircling ductus but appearing flat and twisted, ductus seminalis originating just anterior to sclerotization; corpus bursae largely spinulose, *with two equal-sized finlike signa.*

Discussion. *Gretchena garai* is distinct from all known congeners because of the green scaling on thorax and forewings, and the absence of setae on the anal extensions of male cuculli. I examined three additional males with the same data as the types but excluded them from the type series because of poor condition. All specimens had some or many forewing scales missing; I could not tell whether they had forewing scale tufts, a generic trait. It seems likely that specimens with all scaling intact would appear greener. The species is named in honor of Robert I. Gara and his forest entomological work in Ecuador.

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INJURY AND BIOLOGY OF THE CLEARWING BORER
SYNANTHEDON KATHYAE ON HOLLY

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ABSTRACT. *Synanthedon kathyae* Duckworth & Eichlin was reared from infested holly cultivars (*Ilex* spp.) at Bridgeton, New Jersey. This is the first reported host for *S. kathyae*. Signs of infestation are wilting, yellowing, and dying foliage. Frass galleries around the root collar and cracked, loose bark at the base of the plant provided further evidence of infestation and injury. There appears to be one generation annually.

Additional key words: Sesiidae, *Ilex* spp., galleries.

When originally described, *Synanthedon kathyae* Duckworth & Eichlin was known only from six specimens collected from Lewisboro and Long Island, New York; Oconee Co., South Carolina; and Halifax, Nova Scotia (Duckworth & Eichlin 1977). Subsequently, one moth was captured in a pheromone-baited (Z,Z isomer of 3,13-octadecadien-1-ol acetate) trap in Kent Co., Maryland (Neal & Eichlin 1983) and three males were trapped with the same attractant in Barnstable, Massachusetts. Nothing was known of its hosts or biology. We report rearing this species from ornamental holly trees commercially grown in Cumberland Co., New Jersey, describe its injury, and outline its biology.

Materials and Methods

This insect first came to our notice in 1981 when we received two mature or nearly mature larvae collected from an American holly (*Ilex opaca* Ait.) tree on 13 October 1981 in Millville, New Jersey. The larvae were identified as *Synanthedon*, but species determination had to await association with characters of the adult.

In fall 1982, a borer infestation in container-grown holly trees (*Ilex* spp.), in greenhouses at Millville was called to our attention. In No-

vember 1982, we began rearing the larval borers to the adult stage for identification, and recording injury and effects on the trees. Sixteen container-grown, four-year-old hollies (all of "Blue Angel" variety), including eight infested trees showing decline symptoms and eight apparently healthy trees, were selected from the Millville tree farm for study. These trees were moved to the Rutgers Research & Development Center at Bridgeton, New Jersey, for close and frequent observation.

Four infested and four healthy trees were placed on wooden platforms under shaded screen emergence cages in a heated greenhouse, and the other eight were placed similarly in the field for natural seasonal emergence. The cages were constructed of wood frames and covered with 18 × 16-mesh galvanized screen wire 0.028 cm diam. to enclose an area of about 0.5 m³. The caged plants were inspected weekly until the first moth appeared, and daily afterward. After moths emerged, the infested plants were dissected to study burrowing habits and gallery dimensions. Adult voucher specimens were deposited in the U.S. National Museum of Natural History, Washington, D.C., and in the collection at the Entomology Department, Cook College, Rutgers—The State University, New Brunswick, New Jersey.

RESULTS AND DISCUSSION

The adult of *S. kathyae* is a bluish black moth with clear wings, yellow body markings, and prominent yellow bands on abdominal segments four and five; a detailed description is presented in Duckworth and Eichlin (1977). The mature larva is creamy white with a dark brown head and light brown spiracles, and ranges from 15 to 21 mm in length. The egg is small, brownish, and oval.

Initial signs of infestation were wilting and drooping of tender terminal and branch shoots. The foliage first became chlorotic to yellowish, and finally brown and curled. Girdled branches sometimes dropped their leaves (Fig. 1), while the rest of the plant remained green. Heavily infested plants exhibited progressive dieback with one or more dying limbs, and eventually the entire plant succumbed. Dieback and mortality were most noticeable in early to mid-November.

Light brown frass was ejected from bark entrances just above the soil line. The frass gradually became coarse granular and accumulated in piles on the ground around the root collar. Raking away frass revealed cracked, loose bark that was easily removed to expose larvae and their tunnels (Fig. 2). Multiple galleries in the wood were common; up to six with pupal exits were observed on single plants 3 to 4 cm in diam. at the root collar (Fig. 3). Plants of this size infested by three or more larvae usually died. Galleries were irregular in shape but oval in cross-section, measuring 4 to 8 mm wide and 5 to 8 cm long. Most galleries

FIGS. 1–4.   Injury and signs of *Synanthedon kathyae*. **1,** Dieback on potted holly; **2,** Galleries at base of main stem; **3,** Pupal exit holes and galleries; **4,** Pupal skin protruding from exit hole.

extended 1 to 2 cm below the soil line and 3 to 7 cm above it. Galleries were usually kept open and clean; few contained loose frass.

Ten male and three female moths emerged between 7 and 17 February 1983 from the four infested plants in the heated greenhouse. Two males and one female emerged 30–31 May 1983 from the infested plants in outdoor cages. Single moths of *S. kathyae* have been captured on 25 and 30 June and 14 July in Massachusetts (not previously reported); 17 and 24 July in New York; 25 June in South Carolina; and 2 July in Maryland (Duckworth & Eichlin 1972). Field emergence dates

reported here are similar to those (May–July) for other clearwing species in the region (Neal 1982, Schread 1965, Wallace 1945, Potter & Timmons 1983, Gentry et al. 1978).

The mature larva prepared for adult emergence by cutting a round exit hole 4 mm in diam., leaving only a thin bark flap as a cap. Pupation occurred head-upward in the gallery. Pupal exuviae protruding from exit holes were easily visible around the root collar and lower branches during the emergence season, and provided additional evidence of infestation (Fig. 4). Galleries, larvae of uniform size, and emergence within a single year suggests one generation per year.

Several varieties of holly were attacked. Records and observations at the holly farm suggest that variety "Blue Angel" (*Ilex* × *meservae*) was most susceptible, followed by "Nellie Stevens" (*I. cornuta* [Lindley] × *I. aquifolium* L.) and "Inkberry" (*I. glabra* L.). The varieties "Blue Prince" (*I. aquifolium* × *I. rugosa* [Schmidt]) and "Blue Princess" (*I. rugosa* × *I. aquifolium*) were less attacked. Stressed and weakened plants appeared more susceptible to borer attack than did healthy, vigorous plants.

A question arises as to where the nursery infestation originated. The plants were started in the nursery at Millville and grown in pots to age 4 years for marketing as either 30–38 cm or 38–48 cm tall plants. The nursery was surrounded by a mixed stand of American holly, oaks, white pine, and an undergrowth of shrubs. The insects might have moved from firewood cut in nearby stands and hauled to the nursery for heating, or moths might have flown from natural infestations in the surrounding woodland.

The nurseryman stated that about 30 percent of the "Blue Angel" variety were infested during 1981–82, amounting to an estimated loss of $6,000.

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THE ROLE OF NECTAR SOURCE DISTRIBUTION IN HABITAT USE AND OVIPOSITION BY THE TIGER SWALLOWTAIL BUTTERFLY

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ABSTRACT. In northern New Jersey, larval hosts of the polyphagous butterfly *Papilio glaucus* L. are widely distributed but nectar plants are clumped. Females were rarely captured in an area rich in preferred hosts during the spring generation, when the area lacked concentrations of nectar plants. During summer, second generation females fed and oviposited in the study area while thistles bloomed. The locations of hosts receiving eggs correlated significantly with locations of nectar plants. Such an ovipositional pattern, although probably not maladaptive for larvae, appears to be unrelated to improved larval growth or survival.

Additional key words: Papilionidae, *Papilio glaucus*, adult resources, activity centers.

The distribution of individuals of a butterfly population generally reflects the distribution of their resources. Sources of adult or larval nutrition, or areas facilitating mating or roosting, may all occur in the same habitat as in the Jasper Ridge colonies of *Euphydryas editha* (Ehrlich 1965). In this case the population was local and sedentary (Gilbert & Singer 1973). More commonly, different requirements are met in different habitats. Other populations of *E. editha* were much less localized due to the dispersed distribution of nectar sources (Gilbert & Singer 1973) or local defoliation of larval host plants (Murphy & White 1984). In central Sweden, *Leptidea sinapis* females regularly moved from a woodland nectar foraging habitat to a meadow oviposition habitat (Wiklund 1977). Some habitats that appear to be rich in larval resources may be rarely used (Singer 1971, Cromartie 1975, Chew 1977, Rausher 1979). Areas of otherwise suitable habitat may not be used if they lack a limited resource such as adult nectar plants (Murphy 1983).

In any one habitat, butterflies often do not oviposit on all of their potential larval hosts (Singer 1971, Wiklund 1975, Smiley 1978), nor use all of the habitats in which preferred hosts grow (Singer 1972, Cromartie 1975). Selective oviposition has been interpreted to favor better larval growth or survival (Ehrlich & Raven 1964, Wiklund 1975, Holdren & Ehrlich 1982). Although this has been clearly demonstrated in some cases (Rausher 1980, Rausher & Papaj 1983, Williams 1983), in other cases, no advantage for the larvae has been shown (Chew 1977, Rausher 1979, Courtney 1981, 1982). Certain hosts may favor high

oviposition rates, and higher larval mortality is offset by the greater number of eggs (Rausher 1979, Courtney 1982). If hosts are widely distributed and of similar overall quality, selective oviposition may represent the response of females to other factors such as restricted adult resources (Murphy et al. 1984). This suggests that in many cases the distribution of eggs is a compromise between larval and adult needs.

The tiger swallowtail, *Papilio glaucus* L., is the most polyphagous of the over 500 species of Papilionidae (Scriber 1973), using hosts from over 14 plant families (Tietz 1972). Northern New Jersey is near the limit of bivoltine populations of *P. glaucus* (Hagen & Lederhouse 1985), and in this area, *P. glaucus* females show a strong preference for tuliptree, *Liriodendron tulipifera* L. (Grossmueller & Lederhouse 1987), although several other suitable hosts are abundant (Grossmueller 1984). In northern New Jersey, they also oviposit on the W and S sides of trees within 3 m of the ground (Grossmueller & Lederhouse 1985). Such selective oviposition greatly increases the probability of completing two generations during normal and cooler than normal years. Potential larval hosts are abundant in this area, and *P. glaucus* populations never reach densities high enough to deplete their larval food supply. Our question in the present report was whether the temporal and spatial distribution of adult resources affect which habitats and individual hosts are selected for oviposition.

MATERIALS AND METHODS

The study area was located in Flanders, Morris Co., New Jersey, and consisted of a 5300 m² extension of a larger field (Grossmueller & Lederhouse 1985). It was surrounded on three sides by woods, and had progressed to late old-field succession. Potential hosts such as tuliptree, wild black cherry (*Prunus serotina* Ehrh.), and white ash (*Fraxinus americana* L.) were abundantly scattered throughout the open field, around the edges and in the surrounding woods. The only major source of nectar in or around the study site was bull thistle, *Cirsium vulgare* L., which was in bloom from mid-July through August. The locations of all flowering bull thistles and of all potential hosts within the study site were mapped. The site was divided into 23 plots (10 m × 20 m) to facilitate relocating marked hosts (Grossmueller 1984).

Adult *P. glaucus* were captured and marked from 1 May until 15 September each year of the study. Date, time of day, atmospheric conditions, age, sex, and behavior at time of capture were recorded. No butterflies were removed from the study site. Eggs were sampled four times per week during June through August 1980–82. The upper surface of all potential host leaves at heights of 5 m or less were examined for each host along a 310 m long, 2 m wide transect through the study area. Additional sampling of taller hosts was described in Grossmueller

TABLE 1. Behavior of *Papilio glaucus* adults immediately before capture within the study area.

Brood	Sex	n	Percentage		
			Puddling	Flying	Nectaring
1980-1	Male	43	83.7	9.3	7.0
	Female	4	—	25.0	75.0
1980-2	Male	35	—	11.4	88.6
	Female	42	—	7.1	92.9
1981-1	Male	21	85.7	9.5	4.8
	Female	1	—	—	100.0
1981-2	Male	3	100.0	—	—
	Female	6	—	16.7	83.3

and Lederhouse (1985), but relatively few eggs were laid above 3 m. Because 88.2% of the eggs found within the study area were on tuliptree (Grossmueller 1984), only the relation between the location of tuliptrees on which females oviposited and the location of flowering thistles was analyzed.

RESULTS

Although the study site was selected for its abundance of potential *P. glaucus* larval hosts, only 5 eggs (4.6% of the yearly total) were found in it during the first generation of 1980. Tiger swallowtails were frequently encountered in the area, and 47 were captured and marked. However, 43 (91.5%) of these were males, nearly all of which had been puddling along a swimming pool at the edge of the study area (Table 1). Puddling males form conspicuous groups on moist soil where they ingest sodium, amino acids, and possibly other nutrients (Arms et al. 1974, Berger & Lederhouse 1985).

During the second generation of 1980, 103 eggs were found within the study area. Tiger swallowtails were somewhat more abundant; 77 were captured and marked. The major differences were that only 45.5% of the captures were males, and 90.9% of all captures were nectaring on bull thistle (Table 1). A significantly greater proportion of males captured during the second generation were nectaring (χ^2, P < 0.001). However, the distribution of captured females did not differ by behavior between the two broods. The number of eggs discovered each generation was distributed differently from the total number of *P. glaucus* captures by brood (χ^2, 2 × 2 contingency table, P < 0.001) but did not differ from the distribution of female captures (P > 0.50).

The use of the study site during the first generation of 1981 was similar to that brood in 1980. Of the 22 *P. glaucus* that were captured, 95.5% were male, and 85.7% of the males had been puddling when captured. Only one egg was found during this brood. During June 1981,

the State of New Jersey sprayed the entire Flanders area with a for-
mulation of *Bacillus thuringiensis* to kill gypsy moth caterpillars. Tiger
swallowtail caterpillars are easily killed by this insecticide (Grossmueller
unpubl. results). Only nine captures were made during the second
generation of 1981, and only six eggs were found. However, two-thirds
of the captures were females, which was consistent with the previous
year. The population level of tiger swallowtails continued to be very
low throughout 1982. No eggs were found during the first generation
of 1982, but nine were found at the site during the second generation.

Despite differences in overall population size, the pattern of study
site use was similar from year to year. Although host trees were of
similar availability and quality throughout oviposition periods, females
were attracted to and oviposited within the study area mainly when
thistles were in bloom. Males were attracted to the area to puddle during
first broods, and to feed on nectar when thistles were blooming.

Since blooming thistles attracted females to the area during the second
generation, the influence of thistle location on the particular host plants
chosen for oviposition was investigated. Using the large sample from
the second brood of 1980, numbers of eggs, flowering thistles, and
tuliptree hosts were determined for each of the 23 plots. There was no
relation between number of thistles and number of tuliptrees in the
plots (n = 23, r = 0.12, P > 0.50). Surprisingly, number of eggs was
not correlated significantly with number of host trees (r = 0.11, P >
0.50). Since eggs must be on a host tree, we excluded plots without
hosts from analysis of the relation between eggs and thistles. The number
of eggs was correlated significantly with number of thistles for plots
with at least one host (n = 17, r = 0.55, P < 0.05).

A modified nearest-neighbor analysis was used to compare the mean
distance of each egg (n = 108) to the nearest thistle. The nearest-
neighbor value was 0.27, which indicates a significant clumped spatial
association between eggs and thistles. The value for all host trees was
0.76, which indicates a random distribution.

DISCUSSION

In the area surrounding the study site, tiger swallowtails are probably
not limited by availability of suitable larval hosts. In northern New
Jersey, many previously cultivated fields have undergone succession as
residential communities have largely replaced agriculture. Many of the
host species are early colonizers of abandoned fields, resulting in young
stands of tuliptree or white ash. Even at high population levels, *P.
glaucus* uses only a small portion of available hosts. For example, in
the second brood of 1980, there were 108 eggs oviposited on tuliptrees
within the study area. However, there were approximately 50,800 tu-

liptree leaves that were suitable in condition and location for larval development (Grossmueller 1984). Thus, females can afford to ignore entire areas of host plants in favor of areas containing nectar sources.

In contrast, adult nutrition sources are more restricted. Male tiger swallowtails often form large aggregations at puddling sites (Arms et al. 1974). A puddling site was the prime focus of *P. glaucus* activity during the first broods at our study site. In a study of *P. glaucus* behavior in upstate New York, Berger (1986) found much higher frequencies of occurrence near nectar sources than at locations with abundant host plants but devoid of nectar plants. Our impression is that most of the naturalized nectar plants used during both generations in New Jersey tend to be clumped. Native hosts such as basswood (*Tilia americana* L.) and various briars (*Rubus* spp.) are similarly clumped. When larval hosts are widely distributed and adult resources are localized, female activity and oviposition are greatest near the adult resources (Murphy 1983, Murphy et al. 1984).

Tiger swallowtails are capable of considerable movement in a short time (Lederhouse 1982a). Movements in excess of 5 km between captures are not uncommon for marked males, with one detected displacement of over 2 km in 1 h (Lederhouse unpubl. results). Although females could move from host patches to nectar patches and back again, they appear not to move as much as males (Lederhouse 1982a). Since many nectar plant concentrations may be included in suitable ovipositional habitat, such movement may be unnecessary.

Oviposition in areas of increased male activity is often reduced due to male harassment (Shapiro 1970, Lederhouse 1982b). In *Euphydryas chalcedona*, courtship by nectar-feeding males may reduce the number of eggs laid in the immediate vicinity of nectar plants (Williams 1983). However, disturbed females move only short distances to resume oviposition, producing the overall relation of egg location to nectar plant location (Murphy et al. 1984). Whether this pattern is detected (Murphy et al. 1984) or not (Williams 1983) is a function of what scale is used. When harassment does occur, females may balance problems of interference against costs of extra flight to and away from nectar plants.

In our study, the number of males within the study area was similar for the two generations of 1980. Therefore, lack of females and eggs at the site during the first brood was probably not due to avoidance of males. Furthermore, the presence of abundant nectar plants during the second generation attracted females to the area. The difference in number of females within the study area between the two generations largely accounted for the difference in number of eggs discovered. During the second generation, proximity to a thistle or thistle patch increased the probability that a preferred host would have eggs on it.

Thus, nectar availability controls the local distribution of tiger swallowtail larvae in northern New Jersey.

Results from this study and others (Rausher 1979, Courtney 1982, Murphy 1983, Murphy et al. 1984) support the contention that the distribution of eggs in many butterfly species is a compromise between larval and adult needs. The relative importance of various components in this trade-off will determine the nature of the observed ovipositional pattern.

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GENERAL NOTE

PENSTEMON DIGITALIS (SCROPHULARIACEAE), A NEW FOOD PLANT RECORD FOR HAPLOA CONFUSA (ARCTIIDAE)

Additional key words: alkaloid, boschniakine.

The confused Haploa moth (or Lyman's Haploa, *Haploa confusa* Lyman) is common during July in tallgrass prairie habitats in E-central Illinois. However, little information is available on its larval food plants. *Haploa confusa* is not listed by Tietz (1972, An index to the described life histories, early stages, and hosts of the Macrolepidoptera of the continental United States and Canada, A. C. Allyn, Sarasota, Florida, 536 pp.), and Holland (1968, The moth book, Dover Publications, New York, 479 pp.) makes no mention of food plants. Covell (1984, A field guide to the moths of eastern North America, Houghton Mifflin, Boston, 496 pp.) lists only "hound's-tongue" as a food plant. Several herbaceous plant species are commonly called hound's-tongue, but the name best applies to *Cynoglossum officinale* L. (Boraginaceae), a herbaceous plant of European origin widely naturalized in the United States (Lyons, 1901, Plant names scientific and popular, Nelson, Baker and Co., Detroit, 630 pp.). Other *Haploa* species feed on a variety of plants, including *Eupatorium* (Compositae), *Salix* (Salicaceae), and *Triosteum* (Caprifoliaceae) species (Holland, above).

Foxglove penstemon (*Penstemon digitalis* Nutt., Scrophulariaceae) is a common biennial forb in tallgrass prairie habitats of the Ecological Research Area maintained near Urbana, Illinois, by the University of Illinois. Other dominant plant species in the habitat include big bluestem (*Andropogon gerardii* (Vitm.), Gramineae), Indian grass (*Sorghastrum nutans* (L.), Gramineae), and lespedeza (*Lespedeza cuneata* (Dum.-Cours.) G. Don, Leguminosae) (Lindroth & Batzli, 1984, J. Mamm. 65:600–606). On 1 May 1984, while collecting *P. digitalis* for analysis of alkaloid constituents, I found a second or third stage larva resting on a *P. digitalis* rosette leaf. The leaf was partially eaten and some larval frass adhered to it. The larva was taken into the laboratory and reared through its remaining stadia on leaves of *P. digitalis*. The larva was maintained in a glass Petri dish and fed clumps of rosette leaves until the final stadium, at which time I transferred it to a small Plexiglas cage covering a potted *P. digitalis* plant. The larva exhibited an unusual feeding behavior; it started feeding at the tip of a leaf, then cut a narrow (<1 cm) swath down the center of the leaf, consuming the midrib and a narrow band of tissue on both sides. After pupation, the insect was not visible on the plant or soil surface. Two to three weeks after pupation, a female *H. confusa* emerged.

Use of *P. digitalis* by *H. confusa* is interesting because the plant contains especially high levels of boschniakine (a pyridine monoterpene alkaloid) during the larval feeding period (Lindroth et al., 1986, Biochem. Syst. Ecol. 6:597–602). Alkaloids commonly occur in the food plants of *Haploa* species, including cynoglossophine, heliotrine, lasiocarpine, and platyphilline in *Cynoglossum officinale*, and echinatine and trachelanthamidine in *Eupatorium maculatum* L. (Willaman & Li, 1970, Lloydia 33, Suppl. No. 3A:1–286). In addition to alkaloids, *Penstemon* species commonly contain a variety of iridoid glycosides, such as ajugol and catalpol (Junior, 1983, Planta Medica 47:67–70), although it is not known whether *P. digitalis* contains the compounds. Both alkaloids and iridoid glycosides are deterrent or toxic to many insects (Robinson, 1979, pp. 413–448 *in* Rosenthal & Janzen, Herbivores: Their interaction with secondary plant metabolites, Academic Press, New York, 718 pp.; Bernays & De Luca, 1981, Experientia 37:1289–1290). Thus *H. confusa* larvae probably have physiological or biochemical adaptations that enable them to avoid the effects of these potentially toxic compounds. Alkaloids and iridoid glycosides are sequestered as defensive compounds in other lepidopteran species (Duffey, 1980, Ann. Rev. Entomol. 25:447–477; Bowers, 1980, Evolution 34:586–600). The apparent aposematic coloration of *H. confusa* larvae, black with orange longitudinal stripes, indicates that they may sequester alkaloids or iridoid glycosides from *P. digitalis*.

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BOOK REVIEWS

MEXICAN LEPIDOPTERA: EURYTELINAE I, by R. de la Maza E. and R. Turrent D., color photographs by R. Doniz. 1985. iii + 44 pp., 43 maps, 19 plates (8 in color), 4 unnumbered halftone photos in text. In English. Sociedad Mexicana de Lepidopterologia, AC Publicaciones Especiales 4. Distributed exclusively in United States by Entomological Reprint Specialists, P.O. Box 77224, Dockweiler Station, Los Angeles, California 90007. Paperbound, $25.

Not since the *Biologia Centrali Americana* and Seitz' *Macrolepidoptera of the World* has Mexico's diverse lepidopteran fauna been reviewed. The present work is the first in a proposed series to rectify that situation, the authors' intent ". . . to make the Mexican Lepidoptera known internationally." They chose, for their initial volume, the subfamily Eurytelinae (family Nymphalidae), a group about which a number of generic revisions and life history studies covering Mexican species have appeared during the past 40 years.

There are good points to the work. A male genitalic drawing and at least one color photograph illustrates each of the 44 species (*Perisama mexicana* Hoffmann, known from but a single specimen, receives only a halftone photo in the text section). There are no female genitalic drawings. Seven new subspecies are described and illustrated with halftone photographs. The new forms are based on minor differences in coloration, though genitalic characters are sometimes mentioned but not elaborated. The diagnoses fulfill the Rules of Zoological Nomenclature but I should like to see a supplemental paper presenting more detailed comparisons with related subspecies. Particularly valuable are species keys, drawings of wing nomenclature and venation (Plate II), and diagnostic drawings of hard-to-differentiate species in *Diaethria* and *Myscelia* (Plate I). Also, a distribution map is given for every species. Part IV admirably summarizes recent literature on known food plants and immature stages. Because such data are available for only 14 species in 12 of 16 genera covered, the authors indirectly point to the need for additional research on immature stages.

Unfortunately, annoying problems seriously reduce the work's value. I emphasize, however, that most of these involve presentation, not content. Abundant typographical and grammatical errors make the reading almost painful. For example, on p. 33 there appears, ". . . drinking in wet rocks and mudd, and resting on shaddy roks of the creek wall . . . ." I cannot determine whether the authors or a third party wrote the English version (more than once, the Spanish *y* appears instead of *and*). At any rate, for Entomological Reprint Specialists to have permitted a presentation so ineptly edited to go to press is deplorable.

I appreciate the maps, but they lack localities and outlines of the Mexican States. It appears that three base templates, none with northern or southern borders of the country shown, were used for the maps. Future workers with the Mexican fauna will still have to examine specimen labels and search sparse and scattered literature.

Although the halftone photos are excellent, the color photographs, almost without exception, have shadows (especially dark on Plate XIX). Comparisons with *Moths of North America* (*MONA*) are inevitable, but the quality of the present work does not approach *MONA*'s standards.

Finally, no tribal and generic keys nor synonymies at any taxonomic level are provided. The species keys are clear and easy to use, and perusal of the photographs suffice for species identification. However, the work could have advanced the art and science of euryteline systematics had it carefully outlined supraspecific group differences beyond the brief, noncomparative summaries provided. Omission of synonymies seems inexcusable.

In summary, this first offering in the series goes far toward filling an important gap in our knowledge of world Lepidoptera. As such, the work must take its place beside the few omnibus reviews now available. If only care had been taken to imbue it with more production quality.

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NOCTUELLES ET GÉOMÈTRES D'EUROPE, Volume II, by Jules Culot. Republication by Apollo Books, Lundbyvej 36, DK-5700-Svendborg, Denmark. 243 pp., 81 color plates. DKK 1,380.- for Vols. I–II, and also for Vols. II–IV. DKK 2,500.- for all four.

This book and its companion volumes are a complete facsimile of the original edition (1909–1920) of Culot's work without additional text. The language is French. This particular volume covers quadrifine noctuid subfamilies and a significant proportion of the trifines: Cuculliinae, Heliothinae, some Hadeninae, and some Amphipyrinae. Vol. II completes Noctuidae, and the remaining two cover Geometridae.

For each species covered there are diagnoses and brief details of distribution, biology, and phenology. All are illustrated in color with Culot's skilled and accurate artwork.

At the time of publication, the series was intended to give a complete coverage of the two families for Europe. The author was in contact with notable lepidopterists of his time, particularly Charles Oberthür, and the work was well received by contemporary reviewers who commented both on the crying need for such a work and on the then unsurpassed quality of the illustrations (Entomol. 42:326–327). It is now presented unchanged to a new readership 70 years after its original publication.

I cannot comment on its value as a collector's item. The vagaries of book collectors are unfathomable; the practicing entomologist can only fulminate when useful but old and rare books are sold at prices inflated beyond the range of his pocket. But both will consider the quality of the color plates, the former on faithfulness to the original, the latter on faithfulness to life. The former is likely to be more disappointed because the reproductions lack some of the vivid quality of the originals, and some, but by no means all, have acquired an unfortunate fine speckling. The silvery white patches on some *Cucullia* species on Plate 62 have become clouded with pale ochreous brown, perhaps because the printer considered the accurate originals to look "washed out".

Even with this loss of quality, the practicing entomologist will find that the illustrations stand comparison with most similar modern artwork and reproduction. However, as a means to identification, skilled reproduction of sharp, accurate color photography must take precedence.

The nomenclature used in the work has, of course, become dated in many instances, particularly generic combinations. The book would thus have been much more valuable to practicing entomologists had the publishers commissioned a specialist on European Lepidoptera to write an introductory section including a modern checklist (with cross-reference to text and plates) of the species covered, and comments where advances in systematics have changed the picture (discovery of species complexes), or where further systematic work needs to be done.

Now, as then, there is great need for a modern, comprehensive, authoritative, well illustrated treatment of the European macrolepidoptera fauna, with full investigation of the plethora of scattered type material. Reproduction of a 70-year-old work is no substitute, but it may serve to concentrate the minds of European lepidopterists on the need for a coordinated continent-wide campaign rather than fragmentary regional skirmishes. The proposed *Faunistica Lepidopterorum Europaeorum* (Nota Lepid. 4:90–94) is a promising move in this direction.

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OBITUARY

ARTHUR CHARLES SHEPPARD (1902–1987)

The staff of the Lyman Entomological Museum and all who knew Arthur Charles Sheppard feel a deep sense of loss with his death on 10 March 1987.

Mr. Sheppard was born at Henley-on-Thames, Oxford, England, on 4 August 1902. At the age of 5, he came with his parents to live in Montréal. His formal education in schools was limited; he left school at the age of 13 to obtain gainful employment. He did, however, continue his education at night schools to prepare himself for the business world. He was employed by the Canadian Import Company in Montréal from February 1920 until he retired in April 1968 as Chief Accountant.

Charles Sheppard's father provided the "spark" that initiated his life-long interest and avocation in the world of nature. Together they observed and studied birds on weekly Sunday morning walks. In those days, Montréal was much different than it is now and observations of birds and insects could be made by strolling along Decarie Boulevard. At the age of 9, Sheppard became fascinated with insects and their ways and started his first insect collection.

By 1917, he began more intensive study of insects and exhibited a small collection of butterflies at a Y.M.C.A. hobby show, and similar exhibits at Boy Scout hobby shows. It was at one of these shows that he met Albert F. Winn, then Curator of the Lyman Collection of insects at the Redpath Museum, McGill University. Winn urged him to join the Montréal Branch of the Entomological Society of Ontario, which he did in June 1918. The meetings of the Branch provided the opportunity for the young man to meet many entomologists, amateur and professional. His association with these people with common interests was all that was needed to develop and intensify his enduring interest in the Lepidoptera, particularly of the eastern Canadian species.

Sheppard was Secretary-Treasurer of the Montréal Branch of the Entomological Society of Ontario during 1937 and 1946–49, and Treasurer in 1950. Following revival of the Entomological Society of Québec, he was Treasurer in 1951 and then Treasurer of the Montréal Branch from 1952 to 1954. At the time of his death, he had been a member of the Society continuously for more than 68 years. The Québec Society honored him by conferring on him the status of Honorary Member.

He was a charter member of the Lepidopterists' Society and a member of the Québec Society for the Protection of Birds, since 1935. From 1938 to 1947, he was a member of the Southern California Academy of Sciences.

His association with the Lyman collection of insects began in 1918 and continued over the years as many Entomological Society meetings were held at the Redpath Museum in the "Lyman Room". He was closely associated with George A. Moore, Curator of the Lyman collections after the death of Winn in 1935.

The Lyman collection of insects was moved to Macdonald College in 1961, to become the Lyman Entomological Museum, when I was appointed Curator.

Sheppard's association with the collection continued, and following his retirement from the Canadian Import Company, he was appointed Honorary Curator (Lepidoptera), a position he held until his death. He was also a member of long standing on the Lyman Entomological Committee of McGill University, the committee which served many years as overseer of Museum operations.

Sheppard's work on Lepidoptera was invaluable. The Museum, known since 1972 as Lyman Entomological Museum and Research Laboratory, benefitted not only by his skill and patience in pinning specimens of the tiniest Microlepidoptera and in rearing specimens, but also by his arranging and curation. He donated many thousands of specimens to the Museum, and when the Museum purchased his personal collection (approximately 30,000 specimens) we determined that he had already donated at least that many specimens. The result is that the Lyman Lepidoptera is the finest and most complete collection of Québec lepidoptera in existence. Sheppard also discovered several new species of insects. He described one species, and a number of other species were named in his honor.

All of us who worked closely with Charles Sheppard in the Museum, particularly

Arthur Charles Sheppard

Honorary Curator D. Neil Duffy and I, knew him as a shy, unassuming individual, always ready to share his seemingly endless store of knowledge, yet too modest to accept the credit that he so richly deserved. He was a true and loyal friend and in every way a real gentleman. He will be sorely missed by all of us.

He is survived by his wife Dorothy, daughter Helen (Mrs. C. W. Walker), granddaughters Brenda, Laurie, and Nancy, his sister Dorothy and a number of step-children and their families. We sympathize with them and share their loss.

PAPERS BY A. C. SHEPPARD

1934. A new species of the Genus *Incisalia*. Can. Entomol. 66:141–142.
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1975. Sheppard, A. C. & V. R. Vickery. Types and type designations of North American Lepidoptera in the Lyman Entomological Museum Collection. Can. Entomol. 107:1129–1132.

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PAPERS IN WHICH SPECIES WERE NAMED IN HONOR OF A. C. SHEPPARD

FREEMAN, T. N. 1944. A new psychid from Quebec (Lepidoptera: Psychidae). Can. Entomol. 76:186–187 (*Hyaloscotes sheppardi* Freeman).

MCDUNNOUGH, J. 1929. Some apparently new Microlepidoptera. Can. Entomol. 61: 266–271 (*Phlyctaenia sheppardi* McDunnough [=*Udea sheppardi* (McD.)]).

MCDUNNOUGH, J. 1938. An apparently new *Eupithecia* from eastern North America (Geometridae: Lepid.). Can. Entomol. 70:171–173 (*Eupithecia sheppardata* McDunnough).

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PAPER ABOUT A. C. SHEPPARD

VICKERY, V. R. 1969. A. C. Sheppard, the last of a vanishing breed? Bull. Entomol. Soc. Canada 1(2):20–21.

V. R. VICKERY, *Emeritus Curator, Lyman Entomological Museum and Research Laboratory, Macdonald College, McGill University, Ste-Anne de Bellevue, Québec H9X 1C0, Canada.*

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———— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10:165–216.

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Cover illustration: Semilooping larva of the strange noctuid *Phyprosopus callitrichoides* on *Smilax*. Sketch by Mark Klingler, Carnegie Museum of Natural History. Suggested by John E. Rawlins.

JOURNAL OF

THE LEPIDOPTERISTS' SOCIETY

THE BIG SHIFT: *NABOKOVI* FROM *ATALOPEDES*
TO *HESPERIA* (HESPERIIDAE)

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ABSTRACT.   The orange and brown skipper *Atalopedes nabokovi*, described by Bell and Comstock in 1948 and indigenous to xeric lowland thorn scrub of Hispaniola, is actually a large and stunning species of *Hesperia* with no respect for the classically Holarctic distribution of that genus. Characters of the male and female genitalia are critical both in delimiting the sister genera *Atalopedes* and *Hesperia* and in finding the sister of *nabokovi*. (I compared more than 150 KOH-dissections in these two genera.) Though highly distinct, *Hesperia nabokovi* is genitalically (and ecologically) closest to *H. meskei* of the southeastern United States. Genitalic characters, generally so useful in differentiating species, are also exceptionally valuable at the generic level in skippers. Bell and Comstock, who figured the male genitalia of *H. nabokovi*, must have been misled by the West Indian origin of this skipper and by the large, dark stigma of the male—but even that stigma clearly belongs to *Hesperia*, not *Atalopedes*.

Additional key words: genitalia (male and female), stigma, *Hesperia meskei*, Hispaniola, variation.

Our taxonomy can be wrong where we least expect it. In the course of reviewing the small genus *Atalopedes* before adding a couple of skippers to it (Burns in prep.), I finally obtained specimens of the species endemic to Hispaniola. From the figure of male genitalia in the original description (Bell & Comstock 1948), this species had already struck me as quite the most primitive member of *Atalopedes*—the first to arise after the sister genera *Hesperia* and *Atalopedes* split. Except for the fact that the dorsal edge of the valva was almost uniform in height throughout its length, instead of humped near the middle and lower at either end, the genitalia looked like those of *Hesperia*; but certain critical features of the uncus and the penis did not show in the lateral view provided. And then there was the rest of the animal to wonder about. The moment I saw it, it bothered me: though the facies could fit *Atalopedes* or *Hesperia*, the stigma belonged to *Hesperia*. Still, "the

genitalia are the best place to start" (Burns 1985:3). Sure enough, after perusing the first dissection of each sex and the comparative figures in MacNeill (1964), I knew that *nabokovi* is a species of *Hesperia*.

This hurts the common generalization "*Hesperia* is Holarctic" (Klots 1951, Evans 1955, MacNeill 1964, 1975). Now we must say that *Hesperia* is Holarctic and Hispaniolan, which is less tidy but more alliterative—and a healthy reminder that, despite present distributions, *Hesperia* does not have to be northern in ultimate origin. Of course, its tropical occurrence in the heart of the West Indies need not connote some enormous ecologic leap. The southernmost eastern species of *Hesperia* on the continent, *H. meskei* (Edwards), whose range includes not only peninsular Florida but also Florida Keys, inhabits such hot, dry communities as pine woods or barrens and oak scrub or woodland or savanna (McGuire 1982, Burns unpubl.). The *Hesperia* on Hispaniola occupies most of the xeric lowland thorn scrub (A. Schwartz pers. comm.).

Hesperia nabokovi (Bell & Comstock), new combination

Atalopedes nabokovi Bell & Comstock (1948:19). Evans (1955:339); Riley (1975:186).

The long, verbal original description (of one male and one female from Haiti) dealt with little besides facies and its considerable sexual dimorphism. Description of genitalia was confined to the male and, at that, to a figure (left lateral view), except for a single (under)statement: "The male genitalia show specific differences from those of [*Atalopedes*] *campestris* [(Boisduval)], the unci and the terminations of the claspers being different in the two species." Actually, the genitalia show generic differences—in both sexes—from those of *Atalopedes* and thoroughly fit the *Hesperia* mold.

Rather than conventionally redescribe *H. nabokovi*, I will discuss selected characters in connection with its proper generic placement, its situation within *Hesperia*, its peculiarities, and its variability. Genitalic terminology largely follows MacNeill (1964).

Male Genitalia (Figs. 1–7)

In *H. nabokovi*, as in half the Nearctic species of *Hesperia* (MacNeill 1964), the uncus forms a slender, caudally produced, medial beak— the fine, median dorsoventral cleft at its apex becoming relatively long (Fig. 1). To correspond with the uncus, the paired underlying gnathos lengthens (Figs. 1, 2). As in *Hesperia* generally, the valva ends in two, more or less prominent, pointed dorsal teeth whose bases are connected on the outer surface of the valva by a smooth and conspicuous U-shaped edge (Fig. 2). From the distal tooth, an irregular dentate edge—the
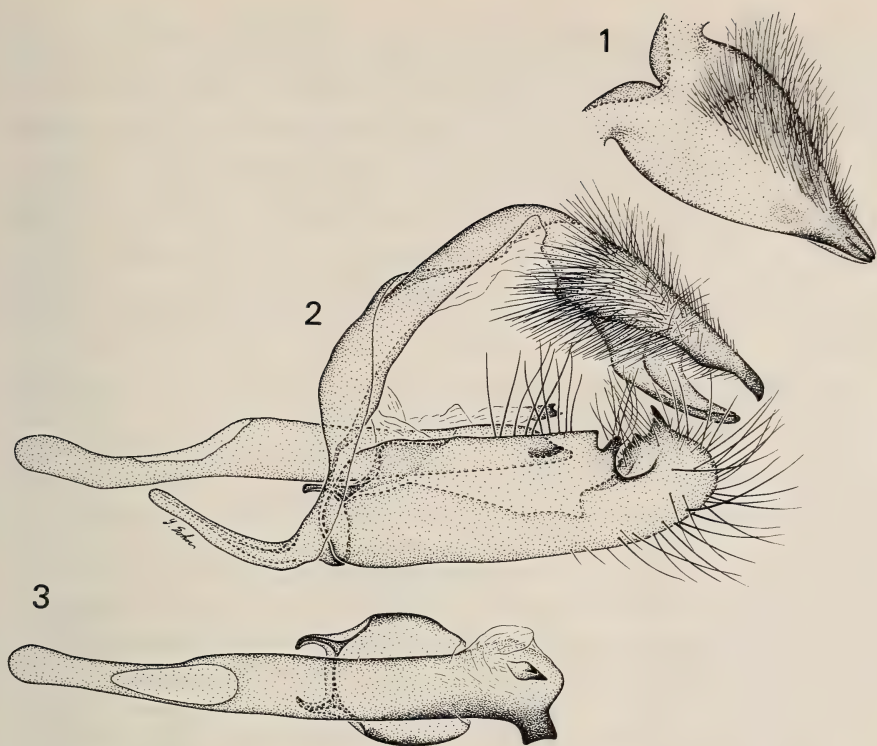
FIGS. 1–3.   Male genitalia of *Hesperia nabokovi* from 4 km E El Limón, ca. 185 m (600 ft), Independencia, Dominican Republic, 16 October 1983, A. Schwartz (genitalic dissection no. X-2196). **1,** Tegumen, uncus, and gnathos in dorsal view; **2,** Complete genitalia (minus right valva) in left lateral view; **3,** Penis and juxta in dorsal view. These figures show certain structures in parallel alignment at two different angles, 90° apart, so as to convey form in three dimensions.

"inner serration" of MacNeill—runs ventrad and cephalad, medial to the proximal tooth (Fig. 2). Again in the *Hesperia* pattern, the penis bears a small, bidentate cornutus distally in the dorsal vesica and a larger, bidentate projection left-laterally at its distal end (Figs. 2, 3). This projection MacNeill (1964) called the rostellum; but I prefer the more suggestive loose synonym titillator (Tuxen 1956), especially on account of its striking hypertrophy in *H. nabokovi* (Fig. 3). The penis is no longer than the rest of the intact genitalia from the anterior tip of the saccus to the posterior tips of the uncus and valvae (Fig. 2). As in other *Hesperia* (figures in Skinner & Williams 1924b and Lindsey et al. 1931), paired prongs projecting anteriorly from the anterior end of the juxta are long and delicate (Figs. 2, 3).

In *Atalopedes*, by contrast, the uncus is stubby; the gnathos, moderate to vestigial; and the valva, elongate, with neither the inner serration of all species of *Hesperia* nor the decided dorsal hump of virtually all of them (so that, in lateral view, top and bottom of the valva are about parallel). The penis—which is much longer than the rest of the genitalia—has either two, relatively elaborate, multidentate cornuti or none at all. The paired prongs projecting anteriorly from the anterior end of the juxta are comparatively short and stout (Burns in prep.).

With respect to these many and various characters, *H. nabokovi* resembles *Atalopedes* only in having an elongate valva without a dorsal hump.

Owing to its long, beaked uncus and long gnathos, *H. nabokovi* goes with an array of *Hesperia* species treated by MacNeill (1964) as "the Metea species group," on the one hand, and as "species of uncertain affinities," on the other. The former includes *H. attalus* (Edwards), *H. metea* Scudder, and *H. viridis* (Edwards); the latter, *H. meskei*, *H. dacotae* (Skinner), *H. lindseyi* (Holland), *H. sassacus* Harris, *H. miriamae* MacNeill, and *H. nevada* (Scudder). These latter species "constitute a very diverse and possibly unnatural assemblage. The morphological divergence apparent between these species is of a magnitude found between species groups elsewhere in the genus" (MacNeill 1964: 157).

The last three species (*sassacus*, *miriamae*, and *nevada*)—which are all adapted to cold—differ from *nabokovi* on various genitalic counts. What may be the most critical involves the point where the paired gnathos joins the tegumen—the "gnathos insertion" of MacNeill—which is much farther forward in these than in any other species of *Hesperia*, including *nabokovi*. Moreover, the uncus beak is exceptionally long in both *sassacus* and *nevada*; and the cleft in its apex is lengthened in *sassacus* and eliminated in *nevada* (a state unique in the genus).

The next two species (*dacotae* and *lindseyi*) also differ from *nabokovi* in many respects, not least of which is a tendency of the titillator to enlarge more posteriad than laterad and to develop additional teeth. This is carried to an unparalleled extreme in *dacotae*, whose hypertrophied titillator extends straight back beyond the distal penile opening to yield the longest penis in the genus.

On the basis of shape and length of tegumen and beaked uncus, length of the uncal cleft, and length of gnathos and level of its insertion, *nabokovi* most nearly resembles *meskei* and the species of the Metea group (*attalus*, *metea*, and *viridis*). These last three species, though grouped, "are not very closely related" to one another (MacNeill 1964: 151); and their nearest (but distant!) ally may be *meskei*: "this species

is not placed easily within any of the preceding groups of species, although it perhaps resembles the Metea group more closely than it resembles any of the [other] species [of uncertain affinities]'' (MacNeill 1964:157). *Hesperia nabokovi* apparently belongs in a section of the genus comprising scattered remnant species. MacNeill (1964:13, pers. comm.) considers them some of the oldest in *Hesperia*. To generalize from present geographic distributions, these species are especially tolerant of heat.

Having roughly rooted *H. nabokovi*, I must hasten to emphasize that it not only lacks close relatives but flaunts more than its share of genitalic idiosyncrasies. The vinculum is uniquely narrow where it joins the tegumen—a feature best seen in lateral view (Fig. 2). The tegumen is uniquely long in the zone of dense bristles, which extends back to about the uncus and the gnathos insertion (Figs. 1, 2). The valva is elongate, with little or no hump on its dorsal edge (Fig. 2). (The nearest approach in other *Hesperia* to this anomalous humpless condition is in *dacotae*.) In dorsal view, at or a little beyond the level of the distal end of the juxta, the valvae are not characteristically "plump" as they are in other *Hesperia*. The broadly rounded distal end of the valva protrudes appreciably caudad of the distal tooth—more so than in any other *Hesperia* (Fig. 2). Last but not least, the hypertrophied, almost rectangular, heavily sclerotized titillator expands to the left from the distal end of the penis like a small, stiff flag on a stout pole (Fig. 3), the two titillator teeth typical of other *Hesperia* becoming the outer corners of the flag.

In their revisions of *Hesperia*, both Lindsey (1942) and MacNeill (1964) stressed the extraordinarily high levels of individual variation encountered. Naturally enough, such variation can loosen the genitalia as well as the external phenotype. Among just three males of *H. nabokovi* at hand, the overall shape of the tegumen plus uncus varies noticeably. From what seems the most nearly average condition (Fig. 1), one male departs in the direction of a malformed tegumen whose transition to uncus is abruptly concave (Fig. 4); the other, in a svelte direction— decidedly longer and narrower (Fig. 5). (Much of the apparent variation in the gnathos, however, simply stems from the mobility of its two separate arms.) Again, in these three males, the proximal tooth of the valva bends inward as little as 20° to as much as 90°, while the distal tooth stays upright (Figs. 2, 6, 7). Because a much-bent tooth vanishes in lateral view (Fig. 7), a casual observer might fail to see the configuration so characteristic of *Hesperia*. Inbending even involves some of the dorsal edge of the valva anterior to the proximal tooth; and, curiously enough, a slight asymmetry crops up, with the left tooth (and rim) bending more than the right. As usual in *Hesperia*, the inner serration
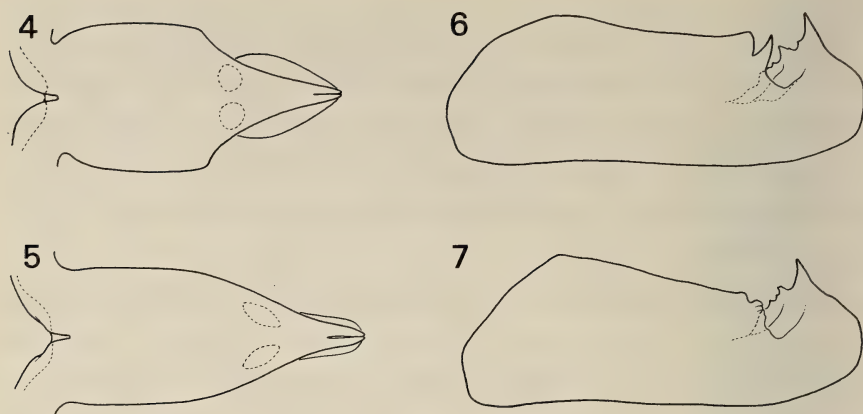
varies in detail (Figs. 2, 6, 7). One male of *nabokovi* starts to express the typical *Hesperia* hump on the dorsal margin of the valva (Fig. 7). The rectangular titillator expands a bit ventrad as well as laterad in two out of three males.

Even though the angle of the proximal tooth varies greatly in *nabokovi*, its orientation relative to the distal tooth (within a single valva) has taxonomic merit. In the nine males of *H. meskei* examined, the proximal tooth bends inward about 15 to 30° while the distal tooth stands erect. Essentially, then, in both *nabokovi* and *meskei* the proximal tooth is medially inclined whereas the distal tooth is about vertical so that, in posterior view, their paths seem to meet or cross. On the contrary, in *H. metea*, *H. viridis*, and *H. attalus* (the Metea group), both the proximal tooth and the distal tooth are medially inclined—and to similar degrees—so that, in posterior view, they look about parallel. Moreover, in lateral view, despite ample variation, the proximal and distal teeth are relatively far apart in *nabokovi* (Figs. 2, 6, 7) and *meskei* but close together in the species of the Metea group (especially *metea* and *attalus*); the proximal tooth is shorter than, or, at most, equal to, the distal tooth in *nabokovi* (Figs. 2, 6, 7) and *meskei* but taller than the distal tooth in the Metea group; and the inner serration, at its proximal end, is not toothed in *nabokovi* (Figs. 2, 6, 7) and modestly toothed in *meskei* but strongly toothed in the Metea group. Again, in lateral view, the U on the outer surface of the valva connecting the bases of the proximal and distal teeth is so deep in *nabokovi* (Figs. 2, 6, 7) and *meskei* that it exposes most of the inner serration but so shallow

in the Metea group that it hides it. All things considered, *nabokovi* is closest to *meskei*.

Female Genitalia (Figs. 8, 9)

Both *Hesperia* and *Atalopedes* reflect a broader pattern in which the sterigma and the ductus bursae are sclerotized while the corpus bursae is membranous.

In *H. nabokovi*, as in *Hesperia* generally, the outline of the lamella postvaginalis is roughly rectangular in ventral view (Fig. 8), the ductus bursae is angled to the left (Fig. 8), a singular expansion of the ductus bursae—corresponding to the "caudal chamber" of MacNeill (1964)— is asymmetrically developed on the right (Figs. 8, 9), the ductus bursae is still sclerotized not only where the ductus seminalis joins but also well cephalad of that level (Fig. 9), and the corpus bursae is roughly spherical (Figs. 8, 9).

In *Atalopedes* a sclerotized midventral prong (short to long, according to species) projects caudad, or caudad and ventrad, from the posterior part of the lamella postvaginalis. The rest of the lamella postvaginalis comprises (1) midventral sclerotization that carries the dorsal wall of the ductus bursae back to the base of the prong, and (2) a closely flanking pair of large, smooth "plates" (variously ovate to comma- or kidney-shaped) that spread dorsad and laterad. Depending on the species, sclerotization of these plates may be strong throughout or so weak that only their medial margins show. In any case, seen ventrally, the lamella postvaginalis as a whole does not suggest a rectangle. The ductus bursae— which is neither angled nor asymmetrically developed—does not enter the corpus bursae directly but by way of a dorsal jog. The ductus seminalis joins the ductus bursae at this jog, which is membranous (coming right after the sclerotized portion of the ductus bursae). The elongate corpus bursae looks like a sausage (Burns in prep.).

The female genitalia buttress those of the male in suggesting that *H. meskei* is the nearest living relative of *H. nabokovi*. In both species the sterigma is unusually simple and lightly sclerotized while the caudal chamber of the ductus bursae is unusually expanded and heavily sclerotized. More explicitly, the lamella postvaginalis looks squarish and relatively flat—without bold features of relief—in ventral view. Its light sclerotization is mainly peripheral (distal and/or lateral), leaving an unto barely sclerotized central zone. The lamella antevaginalis is fully membranous (it is partly sclerotized in other species of *Hesperia*— almost always conspicuously and always perceptibly). The caudal chamber is exceptionally large and flat, expanding far laterad (to the right) but not, or not far, ventrad.

Despite some broad similarity of the caudal chamber in *H. nabokovi*
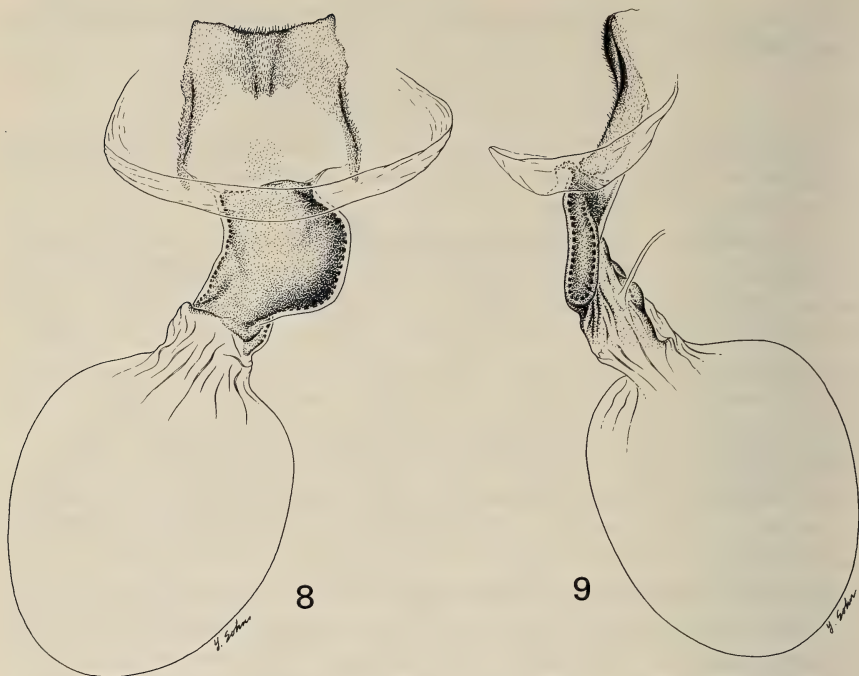
FIGS. 8, 9. Female genitalia of *Hesperia nabokovi* from 1 km SE Monte Cristi, 0 m, Monte Cristi, Dominican Republic, 15 May 1986, F. L. Gonzalez (X-2194). **8,** Sterigma and bursa copulatrix in ventral view; **9,** The same, plus part of the ductus seminalis, in right lateral view.

and *H. meskei*, the ductus bursae as a whole differs a lot. In *nabokovi* it is short; even apart from the caudal chamber, it is wide; and ventrally it is fully sclerotized as far caudad as the start of the lamella postvaginalis. Conversely, in *meskei* it is long; apart from the caudal chamber, it is narrow; and ventrally it is not sclerotized to the level of the lamella postvaginalis. The most striking difference, however, involves such total incorporation of the caudal chamber into the ductus bursae in *nabokovi* that the chamber is no longer the caudalmost element of the ductus (Figs. 8, 9)—a condition unique in the entire genus (compare figures in MacNeill 1964:194, 218–221).

Although the morphologically simpler female genitalia are less glaringly variable than those of the male, they are still highly individual in the three females examined, especially in the outline of the heavily sclerotized caudal chamber, the length and angle of the ductus bursae, and the outline of the lamella postvaginalis. To illustrate, the caudal chamber is somewhat rounded in the female drawn (Fig. 8) but more
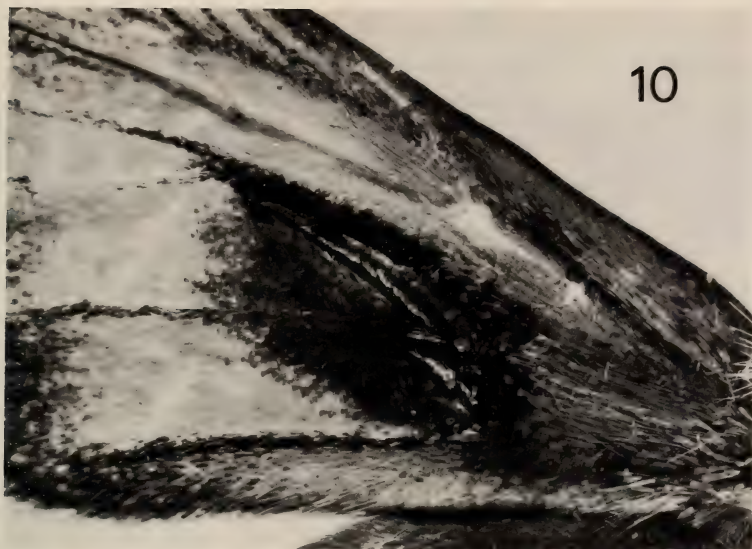
FIG. 10. Stigma on the dorsal left primary of the *Hesperia nabokovi* male whose genitalia appear in Figs. 4 and 6.

rectangular in the other two females, in one of which it is also longer and narrower (as is the entire ductus bursae). Again, in these three females, the midventral third of the posterior margin of the lamella postvaginalis is conspicuously concave, slightly so (Fig. 8), or slightly convex.

Stigma (Fig. 10)

When Bell and Comstock (1948:20) described *nabokovi* in *Atalopedes*, they said "the stigma is relatively very large but of the form characteristic of the species in this genus"; and when Riley (1975:186) treated *nabokovi* in his guide to West Indian butterflies, he said "sex brand as in *A. mesogramma* [(Latreille)]." Not so: the stigma of *nabokovi* carries the *Hesperia* stamp (which has been well characterized by MacNeill 1964:49, 57, 194).

In *H. nabokovi*, the usual parts are present and in place (Fig. 10). Most telling are the two rows of large, wide, silvery-gray scales enclosing the dustlike microandroconial mass to form a conspicuous, gentle arc. Flanking this centerpiece costally and basally are the narrow, dark apical and lower brush patches; and flanking it outwardly is the broad, dark poststigmal patch.

The microandroconial mass is dark gray, as it is in most species of *Hesperia*, not yellow, as it is in the species of the Leonardus group.

Facies (Figs. 11–15)

Essentially, these skippers are orange and brown.

Above, males are mostly bright orange, with a dark outer margin on the primary, a narrow (linear) dark outer margin plus a broad dark costal margin on the secondary, and very narrowly darkened veins in both wings (Fig. 11). The large, dark, central stigma dominates the broadly orange primary—and, for that matter, the entire dorsal aspect (Fig. 11). Two small, orange subterminal spots vaguely mark the inner edge of the dark margin in spaces 4 and 5 of the primary. Below, an unworn male looks mostly dull orange, except for the narrowest of linear dark costal and outer margins on both wings and a very dark basal area (easily hidden) on the primary (Fig. 13). Much of the "dullness" stems from a scaling of orange upon brown: loss of overscaling in worn males reveals a brown ground color across the apex of the primary and over all of the secondary except space 1b and an adjacent strip of space 1c (Fig. 12). The orange overscaling largely obscures pale orange subterminal spots in spaces 4 and 5 and apical spots in spaces 6 and 7 (sometimes also 8) of the primary as well as basal spots and spots of the macular band of the secondary (compare worn and unworn undersides in Figs. 12 and 13, respectively). (Spot terminology follows Lindsey 1942 and especially MacNeill 1964:49, 194.)

As in *Hesperia* and related genera generally, brown coloring develops at the expense of orange in females so as to yield darker skippers. Both above and below, females of *H. nabokovi* show more pattern, more spots than do males (Figs. 14, 15). Spots are opaque. Above, they are orange. But below, the apical and subterminal spots of the primary and the spots of the secondary are white. (Secondary spots include basal spots in the cell and space 7 plus the spots of the macular band, which may extend from space 1c to space 7 when maximally expressed.) Moreover, in unworn females, dark scales ring the white spots of the macular band (Fig. 14), while the overscaling (which covers the same brown ground as in males) has a greenish cast—all to stunning effect.

Although *Hesperia* is a notoriously difficult genus, *H. nabokovi* should not be confused with any other species.

The original description (Bell & Comstock 1948) accurately characterized in many words the facies of a single male and female. The only figures of facies to date are black-and-white drawings (Riley 1975: 186) of those very same specimens. When I lent the holotype male from the Museum of Comparative Zoology, Harvard University, to Riley in 1974 for illustration, its true generic identity escaped me; but, for what it's worth, I can honestly say that I have seen and held the holotype of *nabokovi*.

FIGS. 11–15.   Facies of *Hesperia nabokovi* (all ×1): 11, 15, dorsal views; 12–14, ventral views. **11, 12,** The worn male whose genitalia appear in Figs. 4 and 6 and stigma, in Fig. 10; **13,** The unworn male whose genitalia appear in Figs. 5 and 7; **14, 15,** An unworn female from 4 km SE Monte Cristi, Monte Cristi, Dominican Republic, 18 October 1983, J. W. Raburn (X-2193).

Antenna

In all three males and two of the three females at hand, the nudum of the antenna is 8/5; that is, there are 8 bare segments on the main mass of the club plus 5 on the apiculus for a total of 13. In the third female the nudum is 9/5.

Evans (1955:300, 301, 317, 338) gave the nudum of *Hesperia* as 8/4 and that of *Atalopedes* as 7/7. This character is more variable and more difficult to score than Evans would have you believe.

Size

The length (mm) of one primary in the males is 17.1, 17.5, and 18.6; in the females, 19.0, 20.0, and 20.1. Bell and Comstock (1948:21) gave a primary length of 20 mm for the holotype male and 18 mm for the allotype female.

This is a large species of *Hesperia*.

Spatial and Temporal Distribution

As noted at the outset, *H. nabokovi* occurs in the xeric lowland thorn scrub on Hispaniola, which is extensive. Exact data on the specimens available to me, which come from the northwestern and southwestern Dominican Republic, appear in figure legends. (The one female not specifically cited, genitalic dissection X-2192, has the same data as the male in Figs. 1–3.) The holotype and allotype are from Thomazeau and Fond Parisien, respectively, both in southeastern Haiti (Bell &

Comstock 1948). Altogether, these eight specimens represent six different months—February, May, July, August, September, October—indicating that *H. nabokovi* is multivoltine.

DISCUSSION

Why did Bell and Comstock (1948) put *nabokovi* in *Atalopedes* and not *Hesperia*, especially with so many relevant genitalic illustrations about. Within the preceding quarter century, Skinner and Williams (1924a, 1924b) had figured the male genitalia of *A. campestris* and the American species of *Hesperia*; Lindsey et al. (1931) had reprinted all those figures; Lindsey (1942) had newly refigured the male genitalia of the entire genus *Hesperia*; and Comstock (1944) had figured the male genitalia of *A. mesogramma*. Clearly, Bell and Comstock gave too little weight to genitalic morphology and far too much to the dark color and large size of the poststigmal patch. And (subconsciously, at least) they must have thought Haiti too tropical, too insular—altogether too outlandish—for a Holarctic genus like *Hesperia*. *Atalopedes*, on the other hand, had long been known from the West Indies and from Central and northern South America in the form of *A. mesogramma* and *A. campestris*, respectively.

There was still a lingering reluctance among American skippermen to give the genitalia their taxonomic due. To appreciate this, one need only study the genitalic figures in Lindsey et al. (1931) for such genera as *Polites* (treated as *Talides*) on pages 97 and 101 or *Atrytone* on pages 112, 115, and 119: the genitalia of *P. verna* (Edwards) are in no way a variation on the repetitious genitalic theme of other species of *Polites* nor are those of *A. arogos* (Boisduval & Le Conte) and *A. logan* (Edwards) variations on the different but equally repetitious genitalic theme of other species of *Atrytone*. Eventually, *verna* was moved to the new genus *Pompeius* and all species of *Atrytone* except *arogos* and *logan*, to *Euphyes* by the Englishman Evans (1955).

Genitalia deserve all the respect and attention they can get, which means, in general, that they should be weighted heavily—and (no mere converse) that they should not be used lightly: nowhere are analysis of variation and interpretation in context more important. Genitalia may be remarkably conservative among species in some genera or complexes (even to the point of yielding no diagnostic characters) and yet wonderfully differentiated among species in others. What may amount to a subtle but real interspecific difference in one instance may be nothing more than individual variation in another. And so forth. Every use of genitalia in systematics calls for thorough background investigation. I

have repeatedly answered questions of individual, geographic, and interspecific variation in skipper genitalia by dissecting and comparing large samples (usually both sexes) from many areas, especially in *Erynnis, Celotes, Atrytonopsis, Autochton, Wallengrenia*, and *Pyrgus* (Burns 1964, 1970, 1974, 1983, 1984, 1985, unpubl.).

My small genitalic sample of *H. nabokovi* (three males, three females) looks better in light of the limited and isolated geographic range of this species. And the considerable individual variation evident in this sample looks minor next to the grand and pervasive genitalic divergence that exists between *nabokovi* and all other species of *Hesperia*.

I have stressed from the start that, in both sexes, the genitalia of *nabokovi*—despite their distinctive attributes—are assuredly those of *Hesperia*. In this connection I note that, within the set of diverse species having a long, beaked uncus and so including *nabokovi*, species apparently not closest to it sometimes express character states reminiscent of it. For example, *H. dacotae* tends to approximate the elongate, humpless valva; and *H. nevada*, the hypertrophied titillator, as well as the simple, lightly and peripherally sclerotized lamella postvaginalis coupled with the caudal chamber expanding substantially to the right. Such similar genitalic tendencies will most likely surface independently among species that are still genetically similar.

However that may be, the magical writer and lepidopterist Vladimir Nabokov would doubtless have enjoyed this switch to the type-genus of the family Hesperiidae.

POSTSCRIPT

Thanks to Kurt Johnson and F. H. Rindge, I saw three more females of *Hesperia nabokovi*, and their dissected genitalia, in October 1987: the allotype (from the American Museum of Natural History, New York), which was taken in 1922 at an elevation of about 60 ft (18 m) in Haiti, plus two females taken recently at even lower elevations in the desert around Cabo Rojo, Pedernales, Dominican Republic. Variation in the genitalia is conspicuous, matching what I have already described. With respect to facies, both Cabo Rojo females have "unusually" small spots below; and above, one female is remarkably orange and hence bright, while the other is as dark as the now faded allotype once was. Predictably, the larger sample pushes variation toward the rampant state so common in

Hesperia. Nudum counts are again 8/5 and 9/5; primary lengths, another 20.0 mm and a whopping 21.5 mm.

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LITODONTA HYDROMELI HARVEY (NOTODONTIDAE): DESCRIPTION OF LIFE STAGES

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ABSTRACT. *Litodonta hydromeli* defense structures, mandibular morphology, feeding behaviors and setal morphology differ among instars. The third abdominal SV1 seta is twice as long in the first than in later instars. Later instars have numerous, scattered secondary setae. First instars skeletonize leaves with forklike mandibles. Subsequent instars ingest entire leaves, and their mandibles have a thin, ridged, cutting edge. First instars possess elaborate prothoracic scoli and dorsal spines which are progressively reduced in later instars as a prothoracic gland develops. Larvae spray an acidic substance which deters ants. *Litodonta hydromeli* feeds on *Bumelia* species (Sapotaceae) and developed indoors from egg to prepupa in six weeks. Adults reproduced readily in captivity.

Additional key words: Heterocampini, ontogeny, immatures, defense gland.

Notodontid adults have been described as medium-sized, noctuidlike moths (Forbes 1948), and probably have been neglected in ecological and systematic studies due to their plain appearance. The caterpillars, however, are notable for their bizarre shapes and developmental changes (ontogeny) (Packard 1895, Holloway 1983). As early as 1895, Packard recommended studies of larval ontogeny for systematic purposes. Although coloration and gross morphology have been described for several notodontid immatures (Peterson 1948, Dyar 1904, Godfrey 1984, Godfrey & Appleby 1987), detailed information of setal arrangement and larval ontogeny is lacking for most species.

Litodonta hydromeli Harvey is a north temperate representative of the tribe Heterocampini, and the species occurs in Florida, Texas, Oklahoma and Missouri (Harvey 1876b, Kimball 1965, Stephen Passoa pers. comm.). Harvey (1876a, 1876b) and Packard (1895) gave general descriptions of adult habitus. *Litodonta hydromeli* is figured in Holland (1903, plate 39, fig. 20), Kimball (1965, plate 20, fig. 3), and Packard (1895, plate 5, fig. 16). Dyar (1904) described the eggs and last instar, and gave *Bumelia angustifolia* (Nutt.) (Sapotaceae) as the larval host. Like some other Heterocampini, *Litodonta hydromeli* transforms from a spiny first instar to a cryptic fifth instar with a cervical defense gland (Herrick & Detwiler 1919, Eisner et al. 1972, Weatherston et al. 1979).

The purpose of this paper is to detail larval, pupal, and adult morphology of *L. hydromeli*, and to discuss changes in larval defense structures and feeding biology during development.

METHODS

Adults were taken at blacklights at Austin, Texas, in March 1983, March 1984, September 1985, and April 1986. Females (culture Nos.

W84-102, WE85-25, and WE85-37) were placed in jars and eggs obtained. I reared cultures at 24°C on the leaves of *Bumelia lanuginosa* (Michx.) and an unidentified *Bumelia* species in the laboratory. Eggs and subsequent immature stages were preserved in 80% ethanol. Third, fourth, and fifth instars were killed in simmering water before preservation. Shed head capsules were preserved, and some treated with 10% KOH, dehydrated, and slide mounted for study of chaetotaxy. First and second instars were cleared with cold KOH or 2% trisodium orthophosphate, then stained with chlorozol black (Kodak or ICN) dissolved in 20% ethanol. Means are followed by the range in parentheses, except where ranges do not exist. Setal nomenclature follows Hinton (1946). Male and female genitalia, and male appendages were softened in KOH, dissected in 40% ethanol, and stained. Preparations were mounted in Canada balsam. Voucher specimens are in the National Museum of Natural History, Washington, D.C.

RESULTS

Litodonta hydromeli is multivoltine at Austin, and appears to be multivoltine in Florida also (Kimball 1965). As reported by Harvey (1876b), I found at least three broods to occur in March, April, and September. The moths overwintered as prepupae in the laboratory. Females laid eggs on the leaves and bark of *Bumelia*. Development lasted approximately six weeks from egg to prepupa. Eggs took six to seven days to develop. For all stages, intermolt time was approximately five days. Prepupae turned reddish, entered a wandering stage that lasted one day, burrowed into soil, and formed slight, silk cocoons within earthen pupal cells. In nonwintering individuals, time from prepupa to eclosion was about 17 days. Even in these, the prepupa did not immediately form a pupa within the cell. Emerging adults mated readily in captivity, and a second spring brood was obtained. The fall flight occurred in late August and early September.

Description of Stages

Egg (n = 4). Dome shaped; light blue-green, becoming yellow, then brown, before hatching. Diam. 0.99 mm. Chorion with fine, reticulate sculpturing.

First instar (n = 7). Length 3.1 (2.5–3.7) mm. Head dark brown. Body ground color dark reddish brown; with dark brown scoli and spines. Prolegs and ventral areas yellow green with red flecks, A10 proleg bright yellow. Head diam. 0.6 mm; height of frons 0.2 mm; length of epicranial suture 0.2 mm. Chaetotaxy as in Fig. 1. Mandibles with 3 fingerlike lobes (Fig. 2). Prothorax with dorsal, three-pronged scoli (Fig. 4); scoli rugose, sclerotized base extending to anterior margin of mesothorax; XD1 located on midpoint of second prong; XD2 on anterior margin of sclerotized base beneath and anterior to XD1; D1 between prongs on sclerotized base and D2 ventrad and on margin. Other thoracic primary setae as in Fig. 8. D1 of abdominal segments A1–A6, A8 and A10 on raised, serrate pinacula; SV1 of A3 extremely long, twice length of other setae, ventrally
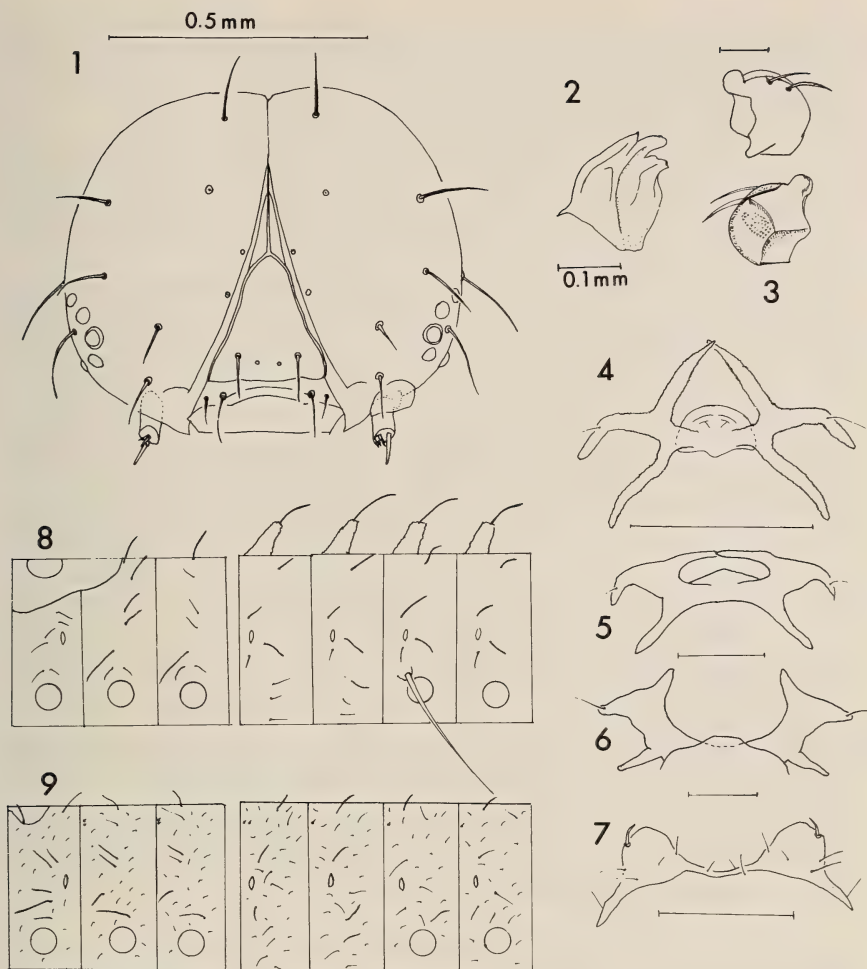
FIGS. 1–9. *Litodonta hydromeli* larval morphology. **1,** Head chaetotaxy of first instar; **2,** First instar mandible; **3,** Fifth instar mandible; **4,** Prothoracic scoli of first instar; **5,** Prothoracic scoli of third instar; **6,** Prothoracic scoli of fourth instar; **7,** Prothoracic scoli of fifth instar; **8,** Chaetotaxy of thorax and A1 to A4 of first instar; **9,** Chaetotaxy of thorax and A1 to A4 of fifth instar. Scales represent 1 mm unless otherwise indicated.

directed. Prolegs on A3–A6 well developed, those on A10 reduced. Crochets uniordinal, uniserial. Chaetotaxy as in Fig. 8.

Second instar (n = 4). Length 3.6 (3.1–4.3) mm. Numerous scattered secondary setae present in this and all subsequent instars. Coloration similar to first instar. Head diam. 0.8 (0.8–0.9) mm; height of frons 0.2 (0.2–0.3) mm; length of epicranial suture 0.4 (0.3–0.4) mm. Mandibles with ridgelike cutting edge. Prothoracic scoli as in first instar but slightly reduced and more stout. D1 of segments A1–A6 and A8 on simple, raised pinacula; D1 of A10 on slightly raised pinacula; SV1 of A3 normal.

Third instar (n = 5). Length 11.1 mm (n = 2). Head dark brown; body green with

sublateral white stripe. Head diam. 1.4 (1.2–1.5) mm; height of frons 0.4 (0.3–0.4) mm; length of epicranial suture 0.7 (0.6–0.8) mm; vertex slightly narrower than in previous instars. Prothoracic scoli reduced, but with three distinct prongs (Fig. 5). Opening of prothoracic gland visible. Coxae with spindle-shaped seta on cephalic, dorsal margin. D1 of A1–A6 on reduced pinacula; D1 of A8, A10 on flat pinaculi.

Fourth instar (n = 5). Length 13.1 mm (n = 3). Coloration similar to fifth instar. Head diam. 2.1 mm; height of frons 0.9 (0.8–1.1) mm; height of epicranial suture 1.1 (1.0–1.1) mm. Prothoracic scoli with reduced prongs (Fig. 6); adenosma well developed; spindle-shaped seta present on all thoracic coxae. D1 of all abdominal segments nearly indistinguishable from secondary setae. A10 prolegs completely reduced, with ring of setae surrounding undeveloped plantae.

Fifth instar (n = 7). Length 34 (32–36) mm. Head brown; body green with white flecks; prothoracic prominences brown; a broad, reddish brown (concolorous green in some individuals) dorsal stripe extending from prothorax to tenth segment; a faint, horizontal, sublateral, white stripe from prothorax to tenth segment; thin, horizontal, midventral and subdorsal white stripes on thorax. Abdominal segments with diagonal white stripes extending intersegmentally. Subventral and underside brown with white flecks. Head diam. 3.3 mm; height of frons 0.9 (0.8–1.1) mm; height of epicranial suture 1.6 (0.5–1.8) mm. Mandibles as in Fig. 3. Hypopharyngeal complex as in Fig. 10; clypeus deeply invaginated with two pairs of stout setae on tip, and two pairs of minute setae on underside. Six larval stemmata; O3 surrounded by enlarged, sclerotized ring. Chaetotaxy as in Fig. 11. XD1 of prothorax on a smooth, conical prominence (Fig. 7). Everted adenosma bifurcate (Fig. 12). Spindle-shaped coxal setae as in Fig. 13. Abdominal chaetotaxy as in Fig. 9, two md microsetae on first abdominal segment. Prolegs on A3 with 30 (21–33) crochets, on A4 with 34 (33–35) crochets, on A5 with 34 (32–37) crochets, on A6 with 35 (34–37) crochets.

Pupa (n = 8). Length 18.2 (15.0–27.0) mm. Vertex with slight indentation. Tb1, Tb2, and Tar3 visible. Caudal edge of mesonotum with row of pits below ecdysial line of weakness. Spiracles with densely packed, short, recurved setae. Cremaster two oblique, outwardly pointing processes.

Adult. Ocelli absent; antenna ⅔ pectinate in both sexes, last 15 segments laminate, pectinations bicolored, black dorsally, ventral extension light brown. Epiphysis ¾ length of tibia. One pair of tibial spurs on mesothoracic legs; spurs with grooved inner surface extending more than ¾ spur length. Metathoracic tibia with two pairs of spurs; first pair with serrate ridges on inner tip surface approximately ⅓ spur length; second pair like mesothoracic one. All tarsi spinose; 5th tarsomere with 2 long, dorsolateral setae. Claws bifid. Male eighth sternite as in Fig. 14; male genitalia as in Figs. 15, 16. Female genitalia as in Fig. 17. Female wing with 5 frenular bristles.

DISCUSSION

Three chaetotaxic changes occur among instars in *Litodonta hydromeli*. First, a spindle-shaped seta on the thoracic coxae appears in the third, fourth, and fifth instars. The function of this seta is unknown. It occurs in mature larvae of *Furcula borealis* (Guér.-Méneville), *Heterocampa astartioides* Benjamin, *Schizura unicornis* (J. E. Smith), *Hyparpax aurora* (J. E. Smith), and *Disphragis* sp.; but not in *Dasylophia* sp., *Symmerista albifrons* (J. E. Smith), *Lochmaeus bilineata* (Packard), *Hapigia* sp., and *Misogada unicolor* (Packard).

Other setal differences between first and subsequent instars of *Litodonta hydromeli* concern secondary setae and length of SV1 on the first abdominal proleg. Scattered, short, secondary setae occur on the head and body in second and later instars. There are secondary setae on larval prolegs in all instars. In the first instar, SV1 on the first
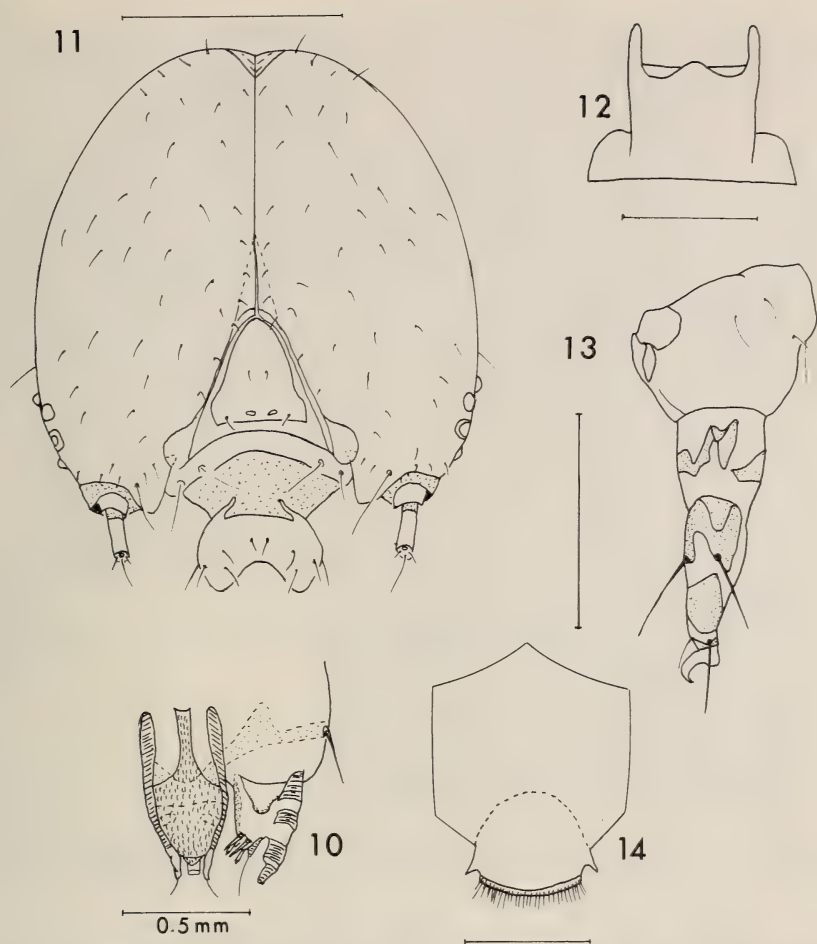
FIGS. 10–14. *Litodonta hydromeli* larval and adult morphology. **10,** Hypopharyngeal complex of fifth instar; **11,** Head chaetotaxy of fifth instar; **12,** Everted adenosma of fifth instar; **13,** Prothoracic leg of fifth instar; **14,** Adult male eighth sternite. Scales represent 1 mm unless otherwise indicated.

abdominal proleg is twice as long as other SV setae (Fig. 8). In all other instars, SV1 is the same length as other SV setae.

    Litodonta hydromeli pupae possess a character found in other North American Heterocampini. Mosher (1917) described the row of deep pits on the pupal thoracic dorsum in *Schizura ipomoeae* (Doubleday), *S. concinna* (J. E. Smith), *Heterocampa guttivitta* (Walker), and *Lochmaeus bilineata* (Packard). These pits also occur in *Schizura unicornis* (J. E. Smith), *Disphragis* sp. (Ecuador, culture No. WE84-007), *Hyparpax aurora* (J. E. Smith), *Heterocampa astartioides*, and one species

FIGS. 15–17.   *Litodonta hydromeli* genitalia. **15,** Male genitalia except aedeagus; **16,** Aedeagus; **17,** Female genitalia. Figs. 15 and 16 are same scale. Scales represent 1 mm.

of Nystaleini, *Strophocerus punctulum* (Schaus). The taxonomic distribution of this character needs further study.

Like *Litodonta hydromeli,* some larval Heterocampini possess elaborate spines in the early instars (Packard 1895), and develop ventral, prothoracic defense glands which become functional in later stages (Herrick & Detwiler 1919, Eisner et al. 1972). Secretions of these glands in *Schizura concinna* and *Lochmaeus manteo* (Doubleday) contain a mixture of formic acid and straight-chain ketones (Eisner et al. 1972, Weatherston et al. 1979). These secretions deter invertebrates and vertebrates (Eisner et al. 1972). Notodontids are the only lepidopterans known to produce defense compounds containing ketones (Blum 1981).

During larval development of *Litodonta hydromeli,* a progressive reduction in the dorsal armature occurs concurrently with the development of the ventral, prothoracic defense gland. The gland can be

dissected out of second and later instars. It is the same shape as that of *Schizura concinna* (Weatherston et al. 1979). The spray of fifth instars has a strong, acidic odor and deters *Atta texana* (Buckley) (Weller unpubl.). The ants vigorously clean their antennae after encountering a larva. However, the spray is not effective against another local ant, *Camponotis* sp.

In addition to ontogeny of defense structures, ontogeny of feeding behavior occurs. Changes in feeding behavior during larval development are correlated with changes in mandibular morphology. First instars feed on the upper surface of the leaf and skeletonize it with forklike mandibles (Fig. 3), whereas subsequent instars ingest the entire leaf, and fifth instar mandibles have a thin, ridged, cutting edge and an inner, roughened surface (Fig. 4). Similar feeding behavior changes are known for several notodontid species (Godfrey & Appleby 1987).

ACKNOWLEDGMENTS

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HOSTS, BIOLOGY, AND DISTRIBUTION OF
ZALE PHAEOCAPNA (NOCTUIDAE)

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ABSTRACT. First-instar *Zale phaeocapna* Franclemont (Noctuidae: Catacolinae), when offered hosts from the immediate environs of the parental female in the Adirondack Mountains, New York, fed on *Corylus cornuta* Marsh. and *C. americana* Walt. (Corylaceae). Two field-collected larvae, compared to the bred larvae and judged conspecific, were beaten from *Ostrya virginiana* (Mill.) K. Koch (Corylaceae) in Florida. A second clutch of larvae was reared on *Hamamelis virginiana* L. (Hamamelidaceae). The larva is described, illustrated, and compared to *Zale minerea* (Gn).

Additional key words: Catacolinae, larvae, *Zale minerea*, Corylaceae.

During field studies near Indian Lake in the Adirondack Mountains of New York, I obtained a gravid female of *Zale phaeocapna* Franclemont which oviposited in captivity. The resulting first instars were offered a selection of plants growing in the immediate environs. *Corylus cornuta* Marsh. (Corylaceae) proved to be an acceptable host. *Acer rubrum* L., *Pinus strobus* L., *Abies balsamea* (L.) Mill., *Larix laricina* (Du Roi) K. Koch, *Alnus rugosa* (Du Roi) Spreng., *Betula papyrifera* Marsh., *Salix rigida* Muhl., and *Prunus virginiana* L., the dominant trees at the site, were not accepted. I have since reared *Zale phaeocapna* repeatedly on *Corylus cornuta* and *C. americana* Walt. from ova of females taken on the Pine Bush Preserve in Albany Co., New York. In addition, I was sent two mature *Zale* larvae collected on *Ostrya virginiana* (Mill.) K. Koch (Corylaceae) in Torreya State Park, Florida, on 22 April 1979. I compared them to my bred *Zale phaeocapna* and determined them to be the same species. Another brood from the Pine Bush locale was switched in later instars to *Hamamelis virginiana* L. (Hamamelidaceae). *Hamamelis* forms buds later than *Corylus*, and its leaves are not present when first instars usually eclose. According to Hall (1952), the Corylaceae possibly were derived from an ancestral stock close to the present-day Hamamelidaceae. Certainly several noctuids can survive the shift from *Corylus* to *Hamamelis* (*Pyreferra* spp.). All the plants known to serve as larval hosts for *Zale phaeocapna* are closely related.

Zale phaeocapna was once a rare insect, originally described from Pennsylvania and Alabama (Franclemont 1950), but is now known from northern New York to northern Florida, and is apparently becoming more common. The moth is abundant on the Pine Bush in Albany, but was not collected there despite intensive collecting in the 1880's on the barrens. The species will come to bait as well as light, so the advent of
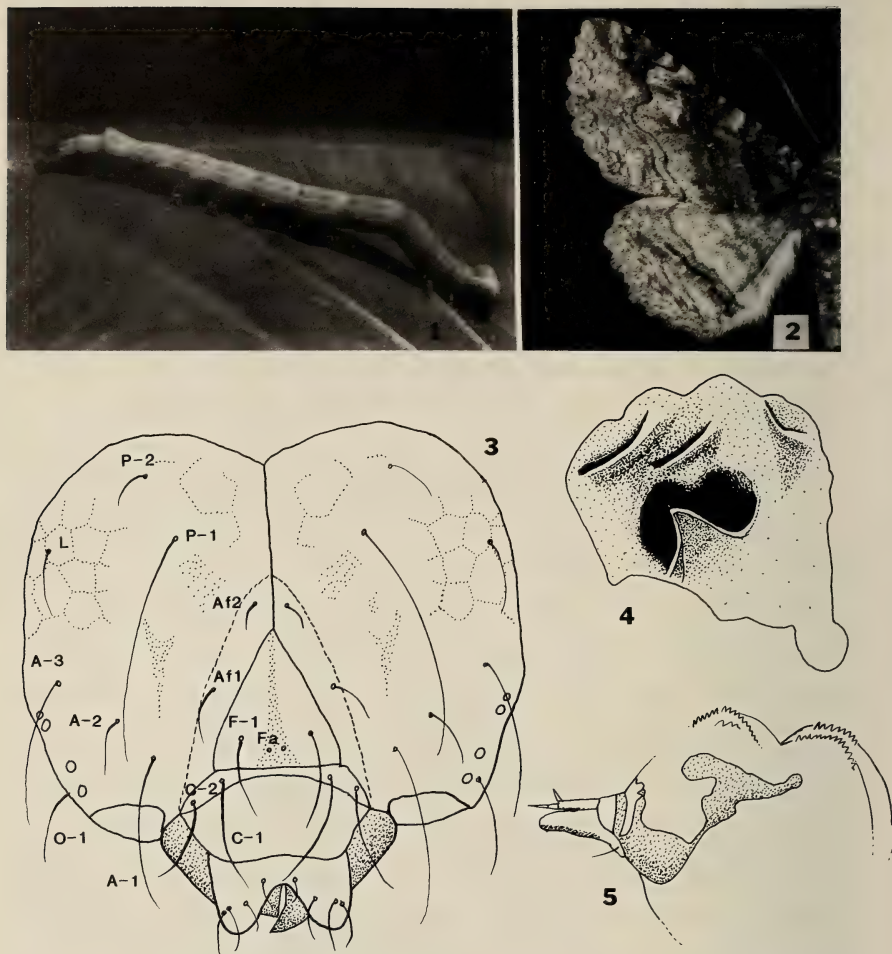
FIGS. 1–5. *Zale phaeocapna.* **1,** Living larva, Adirondack Mts., New York; **2,** Adult; **3,** Setal map and pattern of head. P = posterior head seta, L = lateral head seta, A = anterior head seta, Af = adfrontal seta, F = frontal seta, Fa = frontal puncture, C = clypeal seta. **4,** Oral face of left mandible; **5,** Hypopharynx.

the ultra-violet collecting light does not account for its apparent increased abundance. Baiting was a popular collecting practice in the 1880's and was used on the Pine Bush. The Albany Pine Bush is a sandy, pitch pine–scrub oak barrens, and *Corylus* is a common shrub. *Hamamelis* is uncommon and *Ostrya* is rare, whereas the moth is common. In the immediate locale where *Zale phaeocapna* was collected and reared in the Adirondacks, *Ostrya* and *Hamamelis* were absent.

The parental female oviposited on 21 May 1980, and first stage larvae
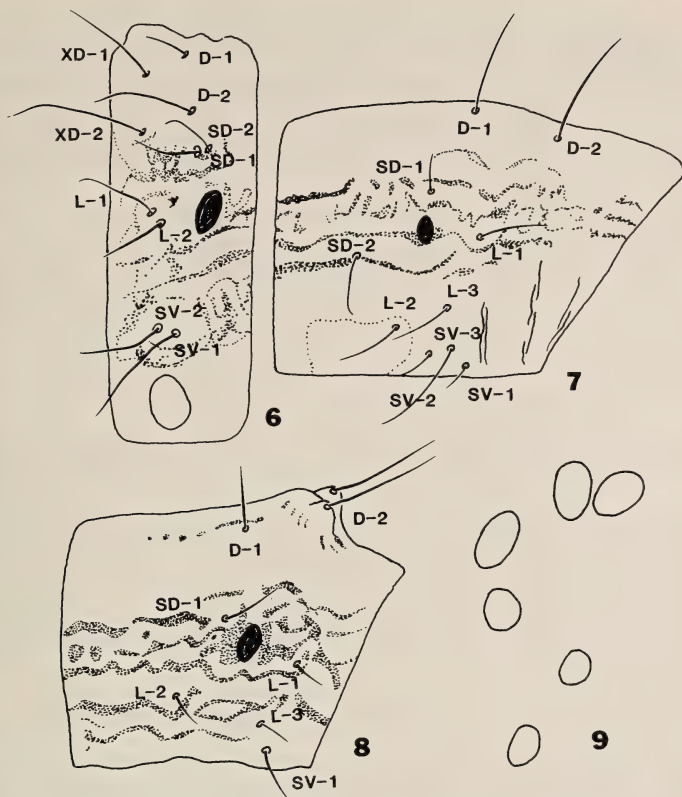
FIGS. 6–9. *Zale phaeocapna.* **6,** Setal map of prothorax, lateral expanded view (from middorsal to midventral line); **7,** Setal map of 1st abdominal segment, lateral view (ventral seta not visible); **8,** Setal map of 8th abdominal segment, lateral view (ventral seta not visible). D = dorsal seta, XD = primary seta, SD = subdorsal seta, L = lateral seta, SV = subventral seta. **9,** Ocellar map.

eclosed 29 May. Fully mature larvae were obtained by 1 July 1980. Larvae were reared in clear plastic containers under ambient conditions. The pupae overwintered and were held in a refrigerator at 4°C until 30 March. Adults began emerging 1 April 1981, suggesting overwintering as a pharate adult within the pupal shell (N = 17), a supposition supported by early spring emergence of the adults in nature. Voucher specimens are in the New York State Museum.

<div align="center">

Description of Mature Larva
(Figs. 1, 3–9)

</div>

Total length 36–40 mm (N = 10). **Coloration** (living material): head silver-gray with irregular dark markings. Body with an alternating blue-gray and yellow striped pattern

as follows: a narrow, yellow dorsal stripe; a broad, blue-gray subdorsal stripe; a broad, yellow supraspiracular stripe; a broad blue-gray spiracular stripe; a fine, narrow, yellow subspiracular stripe.

Head (Fig. 3). Average head width 3.2 mm; epicranial suture 1.6 mm; height of frons 0.75 mm (N = 10). Ocellar interspaces as in Fig. 9.

Mouthparts. Hypopharyngeal complex with distal and proximolateral teeth as in Fig. 5. Mandible with inner tooth and ridges as in Fig. 4. Spinneret extending beyond second segment of labial palpus.

Thoracic segments (Fig. 6). Cervical shield weakly sclerotized; prothoracic spiracle averaging 0.33 mm high.

Abdominal segments. Ab-1 (first abdominal segment) shown in Fig. 7. Crochets a uniordinal mesoseries of 13, 24, 31, 33, and 34 for segments 3, 4, 5, 6, and 10, respectively (rounded to nearest whole number). Ab-8 (Fig. 8) spiracle 0.33 mm high, remaining spiracles 0.24 mm high; spiracles black. D1 (first dorsal) setal bases on Ab-8 markedly protuberant; protuberance slightly higher than height of Ab-8 spiracle.

Material examined. 10 specimens, 10 km E of Indian Lake, Hamilton Co., New York, lat. 43°45′30″ long. 74°10′14″, elevation 555 m.

Diagnosis. In the original description of *Zale phaeocapna*, Franclemont (1950) considered it allied to *Z. minerea* (Gn.) based on adult morphology. Superficially, the adults look like *Z. galbanata* (Morrison), but can be distinguished by the lack of an adterminal bar below M3 on the forewing (Fig. 2). The larvae of *Z. minerea* (based on 10 specimens in the New York State Museum as well as Crumb's [1956] description) compares to that of *Z. phaeocapna* as follows: *Z. minerea* has a much broader oral tooth on the mandible; hypopharyngeal complexes appear the same; *Z. minerea* head capsule maculation is much more extensive, reaching to the front of the head; *Z. phaeocapna* has alternating longitudinal blue-gray and yellow stripes and is narrow-bodied, whereas *Z. minerea* is brown and thick-bodied. *Zale minerea* has been recorded on rose and willow (Crumb 1956), birch and many other trees (Forbes 1954).

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HOST SPECIFICITY AND BIOLOGY OF
PROCHOERODES TRUXALIATA (GUENÉE) (GEOMETRIDAE), A POTENTIAL BIOCONTROL AGENT FOR THE RANGELAND WEED *BACCHARIS HALIMIFOLIA* L. IN AUSTRALIA

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ABSTRACT. *Prochoerodes truxaliata* is an ectophagous foliage feeder native to the western United States. It is multivoltine, with larvae found throughout the year on *Baccharis pilularis*, its only known host. Normal larval development occurred in the laboratory only on species of *Baccharis*, including *B. halimifolia*. Larvae also developed on the closely related *Chrysothamnus nauseosus*, but slow growth and high mortality suggest it is not a natural host. The insect is considered sufficiently stenophagous for introduction into Australia to control *Baccharis halimifolia*.

Additional key words: biological control, *Baccharis sarathroides*, *B. neglecta*.

The woody shrub *Baccharis halimifolia* L. (Asteraceae: Astereae: Baccharineae), an introduction from North America, is a serious weed in Queensland, Australia (Stanley & Ross 1986). The Queensland Department of Lands, through the Alan Fletcher Research Station, has instigated a long-range research program to find biological control agents in the New World for release against this weed in Australia.

One source of potential biocontrol agents is the fauna feeding on species closely related to the weed. Indeed, some authors (Pimentel 1963, Hokkanen & Pimentel 1984) suggest that such insects may be better biocontrol agents because they possess less "ecological homeostasis". Programs against *Opuntia* spp. (Dodd 1929, Fullaway 1954, Pettey 1948) provide examples where insects from hosts other than the target species have given significant control.

Baccharis pilularis is one of 20 United States species of the predominantly South American genus, and is found throughout coastal California and Oregon where two subspecies are recognized. *Baccharis p. pilularis* DC. is a prostrate form found near the coast and often grown as an ornamental. *Baccharis p. consanguinea* DC. is an erect form found further from the coast, and is morphologically very similar to *B. halimifolia*.

Tilden's (1951a) comprehensive survey of the insect fauna associated with *B. pilularis* formed a useful adjunct to the biological control pro-

gram. A number of species listed there were studied further. One, *Rhopalomyia californica* Felt (Diptera: Cecidomyiidae), is already controlling *B. halimifolia* in some areas of Australia (McFadyen 1985). A second, *Trirhabda flavolimbata* (Mannerheim) (Coleoptera: Chrysomelidae), was found to have too wide a host range for introduction; laboratory tests indicated it might breed on *Aster novae-angliae* (Palmer 1985).

A third, *Prochoerodes truxaliata* (Guenée) (Geometridae), is the subject of this paper, which reports studies conducted before permission was sought to introduce the insect for biocontrol purposes. Five of the seven species in the North American genus *Prochoerodes* are general feeders on trees and shrubs. The other two, *P. truxaliata* and *P. amplicineraria* (Pearsall), are so distinct that they may not be congeneric with the others (D. C. Ferguson pers. comm.). *Prochoerodes truxaliata* has been recorded only from *Baccharis pilularis*, although adults have been collected in New Mexico, Utah, Colorado, and Arizona, all outside the range of *B. pilularis*. One specimen of *Prochoerodes amplicineraria* has been reared from *Chrysothamnus nauseosus*.

Botanical nomenclature here follows Bailey and Bailey (1976) or Correll and Johnston (1979).

BIOLOGY

Moths (illustrated in Holland 1968) were nocturnal, emerging from resting places at dusk. They were observed hovering above *Baccharis pilularis* as late as 0100 h at Davis, California. Copulation occurred in early evening and oviposition commenced about three days after eclosion. Unmated females produced sterile eggs. One mated female laid 231 eggs, and after death contained a further 119 undeveloped eggs, for a total brood of 350. Females oviposited on the plant, but as the eggs have little exochorion they usually fell to the ground. Females also oviposited as they crawled on the ground around the plant.

Eggs were pale green, nearly spherical (0.8 mm diam.), smooth and glossy, but fertile eggs turned brown within 48 h. Eclosion occurred in 8 to 10 days at room temperature (26°C).

Larvae left eggs by eating a hole in the chorion without eating the shell, doubled their size by inhaling air, and exhibited negative geotropism by climbing any available object. The following nondiagnostic larval description is given only for special field use. First instars were dark gray with pale lateral vittae. The head was straw colored with numerous small dark dots, the absence of which from the frons gave the appearance of a frontal line. Thoracic legs and prolegs were also straw colored. Second instars were a translucent neutral gray with faint

dark lateral stripes, and lacked the disproportionately large head of the first instar. Third and later instars were brown, which intensified with maturity. Mature larvae were irregularly dotted with dull black, the dots coalescing to form poorly defined dorsal and lateral stripes. Subdorsal pale lines bordered the dorsal stripe, and two irregular light lines extended laterally, forming a margin to the lateral stripe. The first thoracic and abdominal spiracles were orange, often with blue centers. A pair of short fleshy protuberances was present on the fourth abdominal tergite, and there were indications of a second pair of protuberances on the fifth segment. Abdominal setae were black. In the laboratory, mean development times for 7 instars (N = 8) reared on *B. pilularis* were 4, 4, 5, 6, 7, 11 and 12 days, respectively. Two of 10 individuals underwent an 8th instar.

Small larvae created "windows" in leaves but larger larvae consumed foliage from the leaf edge backwards, often consuming the whole leaf. Most larval growth and foliage consumption occurred in the last two instars. Fully grown larvae were 40–45 mm long. Larvae remained on the foliage during the day, but most feeding occurred at night. Resting larvae assumed a typical geometrid posture. Small larvae, when disturbed, dropped and returned on silk strands attached to the plant. Large larvae clung tightly to twigs and were difficult to dislodge. Mature larvae ceased feeding about three days before pupation and sometimes wandered away from the foliage.

Pupation occurred in a slight cocoon made either in the foliage or on the ground. If on the plant, larvae gathered several leaves together with a few strands of silk to form the cocoon. Pupae were obtect, and 15–20 mm long. Larvae were reared on clusters of *Baccharis neglecta* foliage to compare growth of the sexes. Male pupae were lighter (mean 0.21 ± SE 0.04 g, N = 90) than female pupae (0.32 ± 0.07 g, N = 50). Development times from egg to adult averaged 66.2 ± 0.5 (N = 90) and 70.0 ± 0.6 (N = 50) days for males and females, respectively, at 26°C.

There were three generations a year at Davis and Stanford, California, but larvae were present throughout the year, and overwintered in this stage. Large larvae were present at the end of winter, and produced moths in early April. A second generation was seen in mid-summer, and an autumn generation produced moths in October.

Larvae were collected from both subspecies of *B. pilularis*, but infrequently and then usually at low densities (one or two per bush). Very high densities (hundreds per large bush) were occasionally found near Davis, and these severely defoliated plants. The insect has occasionally become a pest of ornamental *B. p. pilularis*.

REARING

A laboratory colony was started and maintained for a number of generations using the following procedure. Wild moths were collected and confined in paper cups for oviposition. Resultant neonate larvae were transferred to clusters of foliage (*Baccharis pilularis, B. halimifolia,* or *B. neglecta*) held in a 37 × 27 × 17 cm plastic shoe box. Approximately 20 larvae were placed on each cluster. They were transferred to fresh foliage twice a week.

Pupae were collected from the container bottom and foliage, and placed with sugar-water wicks and branches of *Baccharis* in a plastic shoe box with the bottom replaced by fly mesh. Eggs fell through the fly mesh, and were collected from paper towelling under the cage. Eggs were refrigerated for about a month without ill effect; moths, larvae, and pupae could also be cooled for at least a week.

HOST SPECIFICITY

Host specificity of *P. truxaliata* was determined by examining pinned specimens in major entomological collections, and conducting laboratory trials to determine oviposition preference, neonate feeding, feeding behavior of late instars, and behavior in a multiple choice situation.

Museum records. Collections at the University of California (Berkeley, Davis, and Riverside); California Academy of Science, San Francisco; Los Angeles County Museum of Natural History; National Museum of Natural History, Washington, D.C.; and American Museum of Natural History, New York, were examined. Most specimens in these collections had been taken at light traps. Limited data on pinned specimens nominated *B. pilularis* as host.

Oviposition preference. Cages approximately 1 m³ were placed in a temperature-controlled glasshouse. Cages contained four potted plants, each of a different species, and each resting in a 30-cm diam. white dish in a cage corner. Sixteen laboratory-reared pupae (6 female, 10 male) were placed in a cup at cage center with sugar-water wicks. After eclosion and oviposition, eggs in the white dishes were counted. The plants were further tended and examined every alternate day, and any larvae present on the foliage were counted. Each cage of four plant species was replicated twice. Egg numbers were analyzed by analysis of variance (using a log N + 1 transformation) to determine differences in ovipositional preference. Four such series using different plant species were studied and separately analyzed.

Prochoerodes truxaliata exhibited an ovipositional preference for some species over others, with *Baccharis halimifolia* being a preferred host (Table 1). Larvae were found only on *B. halimifolia* and *Chryso-*

TABLE 1. Numbers of eggs collected from dishes surrounding potted plants after oviposition, and numbers of larvae observed on plants. Each series replicated twice.

	Mean no. eggs	Mean maximum no. larvae
Series 1		
Baccharis halimifolia L. (Tribe Astereae)	50 a*	25
Chrysothamnus nauseosus (Pall.) Britt. (Astereae)	49 a	20
Aster novae-angliae L. (Astereae)	0 b	0
Bellis perennis L. (Astereae)	2 b	0
Series 2		
B. halimifolia	89 a*	20
Solidago altissima L. (Astereae)	40 a	0
Conyza canadensis (L.) Cronq. (Astereae)	19 a	0
Lactuca sativa L. (Lactuceae)	120 a	0
Series 3		
B. halimifolia	268 a*	3
Chrysanthemum morifolium Ramat. (Anthemidae)	89 a	0
Tagetes lucida Cav. (Tageteae)	89 a	0
Cynara scolymus L. (Cardueae)	39 a	0
Series 4		
B. halimifolia	189 a*	13
A. novae-angliae	18 b	0
Dahlia pinnata Cav. (Heliantheae)	3 b	0
Gaillardia pulchella Foug. (Heliantheae)	4 b	0

* Means separated by different letters differ significantly (<0.05) by the LSD test from other means in the same series.

thamnus nauseosus. Those on the former developed normally to pupation, but those on the latter developed much more slowly and with a very high mortality in later instars, only one larva successfully pupating and producing a normal looking moth.

No-choice feeding of neonate larvae. Five unfed, neonate, laboratory reared larvae were placed in a paper cup with a young leaf of one plant species. Leaves were changed daily and after 72 h survival was assessed. Not all plants could be tested at the one time but *Baccharis halimifolia* was always included as a control with each series. Each treatment was replicated at least three times and, where possible, foliage was obtained from different plants for replication.

Results (Table 2) show that larvae survived only on *B. halimifolia*, *B. neglecta*, *B. pilularis*, *B. sarathroides*, and *Chrysothamnus nauseosus*, and on these species survival was approximately 80%. Larvae did not survive on *Baccharis glutinosa*, *B. bigalovii*, *B. pteronioides*, or on 22 other plant species.

Feeding by later instars. The ability of late instars to develop on three plant species was evaluated. Larvae 20 mm long and approximately 14 days old were selected from a colony raised on *B. neglecta*

Table 2. Survival of neonate larvae after 72 h exposure to leaves of various plant species.

Plant	No. replications	Mean percentage survival
Tribe Astereae		
Baccharis halimifolia	12	80
B. neglecta Britt.	12	79
B. pilularis DC.	6	96
B. sarathroides Gray	3	80
B. glutinosa Pers.	6	0
B. bigelovii Gray	3	0
B. pteronioides (DC.) Gray	3	0
Chrysothamnus nauseosus	3	92
Isocoma wrightii (Gray) Rydb.	6	0
Gutierrezia microcephala (DC.) Gray	3	0
Aster novae-angliae	3	0
Conyza canadensis	3	0
Solidago altissima	3	0
Tribe Anthemideae		
Leucanthemum maximum (Raymond) DC.	3	0
Chrysanthemum morifolium	3	0
Artemisia tridentata Nutt.	3	0
Tribe Heliantheae		
Xanthium strumarium L.	3	0
Parthenium hysterophorus L.	3	0
Helianthus annuus L.	3	0
Gaillardia pulchella Foug.	3	0
Zinnia elegans Jacq.	3	0
Dahlia pinnata Cav.	3	0
Tribe Inuleae		
Antennaria fallax Greene	3	0
Tribe Eupatoreae		
Eupatorium compositifolium Walt.	3	0
Tribe Lactuceae		
Lactuca sativa L.	3	0
Other families		
Vicia faba L. (Fabaceae)	3	0
Lycopersicon esculentum L. (Solanaceae)	3	0
Cucurbita pepo L. (Cucurbitaceae)	3	0
Albizia julibrissan Durazz. (Mimoaceae)	3	0
Delonix regia (Bojer) Raf. (Caesalpiniaceae)	3	0

foliage. Five larvae were placed on foliage clusters of *B. halimifolia,*
Chrysothamnus nauseosus (closely related to *Baccharis,* and on which
neonate larvae were able to feed) and *Aster novae-angliae* L. (more
distantly related to *Baccharis,* and on which neonates had not been able
to feed). At intervals of 2 or 3 days for 14 days, larval lengths were
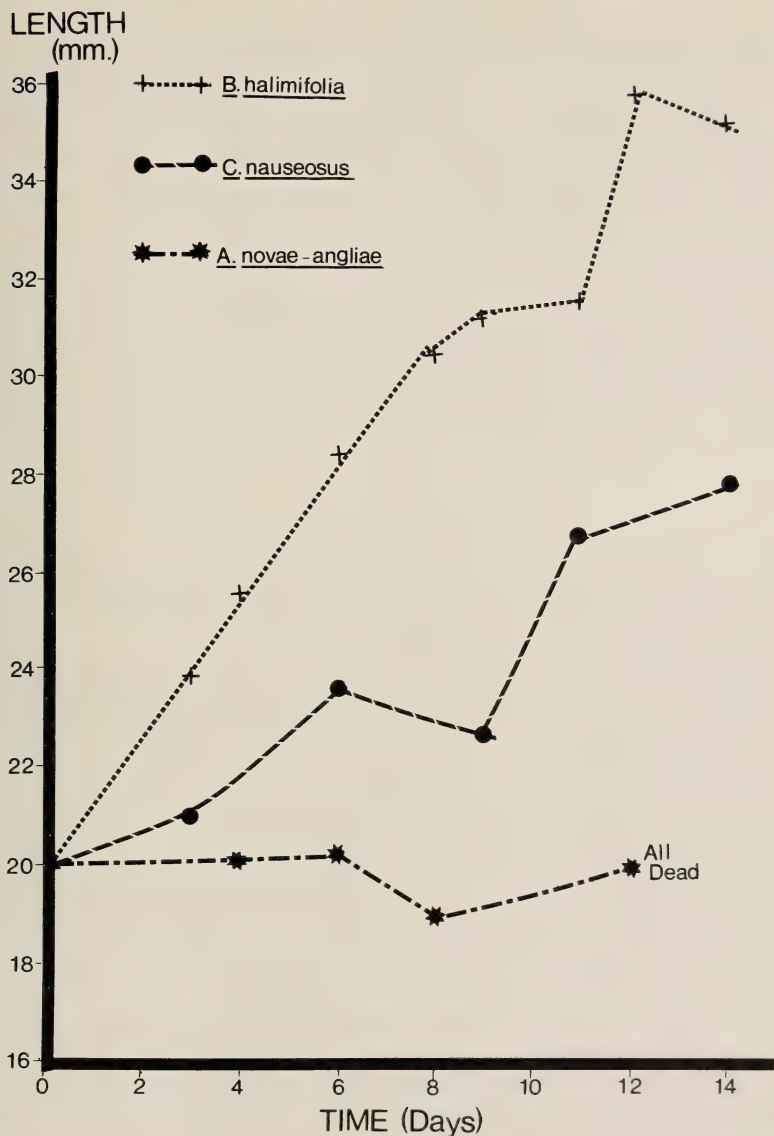
FIG. 1. Growth in length of larvae on *Baccharis halimifolia*, *Chrysothamnus nauseosus*, and *Aster novae-angliae*. Points represent means for 5 larvae.

measured—a simple procedure because larvae naturally assume a stick-like posture on the leaves.

Three distinctively different growth rates resulted (Fig. 1). While larvae survived for up to 12 days on *Aster novae-angliae*, fed somewhat

TABLE 3.   Indices of preference in a multiple-choice experiment with two replications.

Plant	Mean distribution index	Mean percentage foliage consumed	Mean no. leaves nibbled
Baccharis halimifolia (Tribe Astereae)	66	25	27
B. neglecta	13	33	19
Gutierrezia microcephala (Astereae)	2	<1	3
Isocoma wrightii (Astereae)	18	<1	7
Aster novae-angliae (Astereae)	0	0	0
Xanthium strumarium (Heliantheae)	<1	0	0
Dahlia pinnata (Heliantheae)	<1	0	0
Zinnia elegans (Heliantheae)	<1	0	0
Leucanthemum maximum (Anthemideae)	0	0	0
Chrysanthemum morifolium (Anthemideae)	0	0	0
Tagetes lucida (Tageteae)	0	0	0
Gerbera jamesonni Bolus ex Hook (Mutisieae)	1	0	0

on the foliage and produced frass, negligible growth occurred, and after the first few days the larvae looked unhealthy. Those on *Chrysothamnus nauseosus* displayed an intermediate growth rate.

Multiple-choice experiment. A multiple-choice experiment was conducted to determine whether larvae responded similarly on whole plants and cut foliage, and to observe their response when given a choice of plant species. A 53 × 69 × 84 cm cage covered with fly mesh was set up to contain 12 potted plants, each of a different species. Wooden planks were placed above the pots so that foliage and stems protruded through small holes in the planks which acted as a floor and facilitated larval movement between plants. Some hundreds of unfed neonate larvae and eggs were scattered over this floor, simulating the natural distribution of eggs on the ground around plants. The plants were examined daily for the duration of larval development, and the larvae on each plant counted. A distribution index (Palmer 1985) indicating relative larval abundance on each plant was calculated. Number of leaves attacked and an estimate of total feeding were recorded for each plant at the end of the experiment.

Results (Table 3) indicated that *Baccharis* was the preferred host. Few larvae were seen on the non-*Baccharis* plants, and most of them were found in the first few days. None of the other species proved suitable, although some feeding was evident on the closely related *Isocoma wrightii* and *Gutierrezia microcephala*. Toward the end of the experiment, some of the *Baccharis* were considerably defoliated but there was no movement of the large larvae to other plants.

DISCUSSION

Host specificity testing indicated that this insect is highly stenophagous, and that its host range is restricted to *Baccharis* species. Four *Baccharis* species appeared to be equally suitable hosts. This result suggests that *B. sarathroides* may be the host in Arizona, New Mexico, Colorado, and Utah where moths have been collected but *B. pilularis* is not found. A degree of affinity between *Prochoerodes truxaliata* and *Chrysothamnus nauseosus* was also evident, and reflects the phylogenetic relation between *Baccharis* and other North American genera within tribe Astereae. This result, and the host range of another California insect, *Aristotelia argentifera* Busck (Gelechiidae), which is reported only from *B. pilularis* and *Ericameria ericoides* (Lessing) (Tilden 1951b), support the hypothesis of B. J. Turner (pers. comm.) that *Chrysothamnus* and *Ericameria* are the most closely related genera in North America to *Baccharis*.

The insect seems sufficiently stenophagous for biological control use in Australia. It was also tested against a further 6 species in tribe Astereae and another 15 species in other tribes of Asteraceae including most of the commercially important ones. This degree of testing closely related species is greater than commonly done for potential biocontrol agents (Diatloff & Palmer 1987). The partial affinity with *Chrysothamnus nauseosus* is not important in the Australian context because this genus, like most North American genera of the tribe, is not found in Australia. *Conyza canadensis*, *Solidago altissima* and *Aster novae-angliae* are North American species introduced into Australia, and are probably the most closely related of the present Australian flora to *Baccharis*. As such, they might serve as the "critical test species" advocated by Wapshere (1975). Clearly, these plants were not suitable for *Prochoerodes truxaliata*. However, before final clearance for release in Australia, some testing against native species of Tribe Astereae should be undertaken there.

Prochoerodes truxaliata might also be utilized as a biological control agent within the United States. In Texas, *Baccharis neglecta* and *B. salicina*, extremely closely related and often confused (Correll & Johnston 1979), are considered weedy, and have recently been recognized as a management problem on grazing lands (Scifres 1980). It might therefore be possible to introduce the insect into Texas to control these species. It is considered safe for introduction there (R. Bovey pers. comm.).

Although ectophagous Lepidoptera have not been associated with many successful biological control programs, *Prochoerodes truxaliata* does have many desirable features of a good biocontrol agent. It is

multivoltine, highly fecund, capable of causing considerable damage to the host plant, and easily reared in the laboratory. Also, it does not have a strong diapause, a factor which might be particularly useful in Australia where winters are mild. There would appear to be good prospects of this moth establishing on *Baccharis halimifolia* if introduced for biological control.

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GENERAL NOTES

TWO RELATED MIGRATIONS OF THE CALIFORNIA TORTOISE-SHELL BUTTERFLY IN MARIPOSA COUNTY, CALIFORNIA, IN 1986

Additional key words: Nymphalidae, *Nymphalis californica*, hibernation.

Mass exodus flights of the California tortoise-shell butterfly, *Nymphalis californica* (Boisduval) (Nymphalidae), usually follow defoliation of *Ceanothus*, the larval host, in years of abnormal temperatures and subnormal precipitation such as droughts (Shields 1987, Utahensis 7(1):5–13). Years of peak migration in the Yosemite National Park region include 1911, 1922, 1933, 1961–62, 1971–72, and 1986–87. This note reports two related February–May 1986 migrations of *N. californica* near the SW end of Yosemite, and proposes the source to terminus route for the hibernant flight.

In late July 1986 there were extensive migrations for 42 km in the Donner Pass region of Placer and Nevada counties; these flew SW and W (Knaus & Lambremont 1987, J. Lepid. Soc. 41:121–122), independent of the Yosemite migrations in source, timing, and (partially) direction. A syndrome of behavioral, physiological, and ecological characteristics in migratory butterflies follows decreased production of juvenile hormone (Rankin 1978, pp. 5–32 *in* Dingle (ed.), Evolution of insect migration and diapause, Springer-Verlag, New York; Herman & Dallmann 1981, J. Insect Physiol. 27:163–168).

In 1986 at the Shields residence, Jerseydale, 1100 m elev., 14 km NE Mariposa, Mariposa Co., California, sightings were made along a NW–SE 30 m front in a pine forest clearing between cabins. Flight directions were recorded with a hand compass that had been checked against a surveyor's compass. It was placed on level ground and oriented to magnetic N (17½°E of true N) to estimate flight directions. All times were PST.

On 24 February 1986 in Skelton Canyon E of Jerseydale, worn hibernant *N. californica* were abundant (150–200 seen), most muddy areas having at least 10 or 20, sometimes 40 or 50, in mid-morning on a warm, sunny, humid day (22°C). These were from a fall 1985 emigration that had subsequently become resident. A small migration not participated in by residents began on 26–27 February, and was confined to the canyon summit. A heavy rain (500 mm in Mariposa) fell on 15–19 February, followed during 24–28 February by warm, clear, sunny, humid weather (low 20°'s C).

This migration was first noticed on 28 February at Jerseydale (Table 1) beginning at 0930 h and ceasing at 1605 h. Migrants flew up to 15–30 m above the ground, passing over pine trees instead of around them. A few changed direction when reaching the forest; these often appeared in groups of 2 to 4. A resident population (common but nonmigrating) was present at Jerseydale at this time. During March, no migration was seen on overcast days. A maximum migration of 75/h/30 m was reached on 1 March between 1100 and 1200 h (Table 1). After some rain and snow in early and middle March, the migration resumed during 19–27 March with 21–61/h/30 m, reducing to 1–2/h/30 m from the end of March to 22 April. The flight rate (measured by car speedometer) was 32–40 km/h. In unforested areas between Darrah and Big Spring Hill, the flight was only 1–2 m above the ground. By late March many individuals had clear or tattered wings, and by mid-April many were exceedingly worn and flying slowly. In the early morning, the flight direction paralleled the incoming rays of sunlight. On 27 March, migrants were sometimes seen in 3's flying in V-formation. During its peak, migration began at 0920–0930 h and ceased at 1502–1605 h. In late February–early March, it was confined to an area between Jerseydale and Big Spring Hill (11 air km) with none migrating on either side of this front, such as at Briceburg or Mariposa. On 27 March a few *N. californica* were seen migrating ESE at 1100–1220 h on Hunter Valley Mtn., 610–915 m elev., 29 air km NNW of Jerseydale.

TABLE 1. 1986 migrations of *Nymphalis californica* at Jerseydale.

Date	Time (h) (PST)	Predominant direction[a]	Numbers/ 30-m front/h	Percent in predominant direction
Hibernants				
27 February	1420–1500	SE	5[b]	100
28 February	1350–1415	SE	5[b]	100
28 February	1420–1605	ESE	87[b]	100
1 March	1100–1200	SE	75	90
19 March	1250–1350	—	22	—[c]
21 March	1250–1350	SE	61	48
22 March	1100–1200	SE	40	65
24 March	1200–1300	ESE	26	46
26 March	1200–1300	ESE	34	44
26 March	1440–1540	ESE	24	71
27 March	0920–1000	ESE	24[b]	54
19 April	1100–1200	SE	2	100
First Brood				
24 May	1230–1330	WNW	29	38
25 May	0915–1015	E	12	33
25 May	1430–1530	W	14	43
25 May	1530–1630	W	5	80
26 May	0815–0915	—	10	—[d]
26 May	1130–1230	none	8	—
27 May	1430–1530	W	8	38
28 May	1024–1125	W	19	37
28 May	1330–1430	NW	6	33
31 May	1030–1130	W	7	71

[a] Predominant direction refers to greatest percent traveling in any one direction.
[b] Rate/h unknown.
[c] All but one flew SE to ESE.
[d] 40% flew W and 40% flew E.

The source area for the hibernant *N. californica* migration passing through Jerseydale was probably the Vaca Mts. W of Davis. Projecting the SE line of flight backwards intersects this region 230 km from Jerseydale (Fig. 1). There were hundreds to thousands of adults in canyons of the Vaca Mts. in February and March of the migration (A. Shapiro pers. comm.; News Lepid. Soc. 1987, no. 2, p. 17). By May there were fewer larval colonies in the Vacas than would have been expected from their earlier numbers. Projecting their SE line of flight forward from Jerseydale bisects the eastern Sierra Nevada between Lone Pine Creek and Big Pine Creek where D. Giuliani commonly saw nonmigrating adults from 26 February to 11 March of the migration. These were along streams in all canyons from 1980 m down to the valley floor (Fig. 1). None was seen there by 8–11 April 1986. This area is 185 km from Jerseydale and indicates a total of 420 km traveled by part of the migration. The distance between Lone Pine and Big Pine creeks is 65 km, indicating a 6-fold increase in width at the migration's terminus when compared with the Jerseydale–Big Spring Hill width. The rate of travel from beginning to end was 1.5–2.4 days based on 420 km distance, 32–40 km/h flight speed, and 0920–0930 h to 1502–1605 h flight times.

A brief migration of smaller, fresher, first-brood *N. californica* flew through Jerseydale later, in late May 1986 (5–29/h/30 m) (Table 1). On 20 May, 15 fresh adults were flying about, and 5 others were seen migrating. On 21–23 May, days were cool and overcast. The peak flight occurred on 24 May. Flight was near the ground and slower (10–12 km/h) than the hibernant migration. On 26 May along Footman Ridge summit, 1400 m elev.,

FIG. 1.   SE migration of *N. californica* hibernants in 1986.

1 km E of Jerseydale, 6 butterflies were seen migrating W to NW at 0955–1010 h. During late May, migration began at 0838 h and ceased at 1620 h, thus occupying a greater part of the day than the hibernant migration. For 1 h earlier and ½ h later than this, specimens flew back and forth in the clearing and gully, basked, or alighted on trees. By 31 May most migrants were in intermediate wing-wear condition. Migration ceased during the first week of June. Three of 10 specimens collected on 24 May expelled meconia, indicating a nearby source area. This brood was likely the progeny of the hibernant migration. No *N. californica* were seen at Jerseydale during the summer until 25 August when one fresh specimen appeared. A few resident adults reappeared during the fall and early winter of 1986.

Hibernant and first-brood migrations each had their own flight directions (SE vs. W). Greatest variability in direction occurred during breezy weather, with least variability on calm days.

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THE TYPE LOCALITY OF *CATOCALA WHITNEYI* AND REPORTS OF THIS SPECIES IN OHIO

Additional key words: Noctuidae, Catocalinae, distribution.

Catocala whitneyi Dodge has been reported from Ohio several times (Dyar, H. G., C. H. Fernald, G. D. Hulst & A. Busck 1902 [1903], Bull. U.S. Natl. Mus. 52, 723 pp.; Hampson, G. F. 1913, Catalogue of the Lepidoptera Phalaenae in the British Museum, Vol. 12, London, 626 pp.; Forbes, W. T. M. 1954, Lepidoptera of New York and neighboring states, Part III, Noctuidae, Cornell Univ. Agr. Exp. Sta. Mem. 329, Ithaca, New York, 433 pp.; Sargent, T. D. 1976, Legion of night: The underwing moths, Univ. of Massachusetts Press, Amherst, 222 pp.), but my efforts to locate valid Ohio specimens have been fruitless. After exhaustive investigation, I conclude that all previous references to the species occurring in Ohio are erroneous and explainable as misreading the type locality.

G. M. Dodge (1874, Can. Entomol. 6:125–126) described *C. whitneyi,* giving the type locality as "Ohio, Ill." This might be seen as a reference to the states of Ohio and Illinois, but in reality, Ohio is the name of a town in Bureau Co., Illinois. Dodge earlier (1874, Can. Entomol. 6:114–115) referred to Ohio, Illinois, as a single location. That Dodge was referring to this town is confirmed in a letter he wrote to James Angus: "In Bureau County, Ill., I found only *Whitneyi*" (Angus, J. 1884, Papilio 4:35–37).

A credible source for the reports of *C. whitneyi* from Ohio is found in Hampson (above). Hampson lists five specimens and indicates that at least one type specimen is from Ohio: "Hab. U.S.A., Ohio, 1 ♂, 2 ♀ type, Illinois, Nebraska, Kansas (Snow), 1 ♂, 1 ♀." This information contradicts W. Beutenmüller (1907, Bull. Am. Mus. Nat. Hist. 23:145–151) who wrote, "The types of *whitneyi* were unfortunately destroyed by fire, as I am informed by Mr. Dodge, and the specimen in the Grote Collection in the British Museum, supposed to be the type is not one of the specimens from which the description was made." Based on British Museum photographs of the five specimens listed by Hampson, including full label data, none of the specimens is from Ohio. The one specimen bearing a label with the word "Type" simply has the locality as "U.S. America, Grote Coll., 81-116." Two of the other specimens bear labels with data identical to that just cited and two specimens are labeled "Kansas, Snow, Grote Coll., 81-116."

Conceivably, *C. whitneyi* was collected by early Ohio lepidopterists. Charles Dury of Cincinnati and George Pilate of Dayton were accomplished lepidopterists and contemporaries of Dodge. Grote identified many specimens for Dury, and Pilate provided the specimens for Grote's description of *C. dulciola* (Grote, A. R. 1881, Papilio 1:5–6). The connection to Grote is important because one of the Grote specimens of *C. whitneyi* in the British Museum is allegedly a type. Either Dury or Pilate could have provided Grote with *C. whitneyi,* which would account for the Ohio record. This seems unlikely, however, since neither mentioned this species or the similar *C. abbreviatella* and *C. nuptialis* in their papers on Ohio Lepidoptera (Dury, C. 1876, Can. Entomol. 8:187–188; 1878, J. Cincinnati Soc. Nat. Hist. 1:12–23; Pilate, G. R. 1882, Papilio 2:65–71).

Ironically, W. Barnes and J. H. McDunnough (1918, Illustrations of the North American species of the genus *Catocala,* Mem. Am. Mus. Nat. Hist. 3(1), 47 pp.) must have known that *C. whitneyi* had not been recorded in Ohio when they described the distribution this way: "It has only been reported from a few of the Plains States from Nebraska and Kansas northward to southern Manitoba but appears to be fairly plentiful locally." Had they explained the distribution in relation to the type locality, the enigma might have been resolved in 1918.

The recorded foodplant of *C. whitneyi, Amorpha fruticosa* L. (Leguminosae), (Dodge, E. A. 1925, Entomol. News 36:267–268) occurs only infrequently along the Ohio River in western Ohio, but *A. fruticosa* is doubtfully native in Ohio (Braun, E. L. 1961, The

woody plants of Ohio, Hafner, New York, 362 pp.). Another probable foodplant, *A. canescens* Pursh, does not occur in Ohio. However, other species of Leguminosae are found in Ohio along with species of *Catocala* (*minuta* and *illecta*) that use them as hosts. *Catocala whitneyi* has been collected in Kentucky W of Louisville, where *A. fruticosa* is known to occur, but the moth has not been recorded from Indiana.

No Ohio specimens have been located in Ohio collections, nor in major collections including the U.S. National Museum and the American Museum of Natural History. The Museum of Comparative Zoology, where remnants of the Pilate collection are housed, likewise has no Ohio specimens of *C. whitneyi.*

The range of *C. whitneyi* reported by Barnes and McDunnough (above) is essentially correct. A specimen from Tennessee is in the Museum of Comparative Zoology. The range extends N and W through the Plains States including W Kentucky, Illinois, Wisconsin to Manitoba, and W through Missouri, Kansas, Nebraska, and N through the Dakotas. The recorded host, *A. fruticosa*, favors river and stream banks, whereas *A. canescens* is found on sandy soils and prairies. In Wisconsin (L. Ferge pers. comm.), *C. whitneyi* has a decided preference for prairie conditions, suggesting a relation with *A. canescens*; adults rest on the ground during the day.

I thank R. W. Rings and T. D. Sargent for critically reviewing the manuscript, and C. W. Albrecht for encouragement. Many collectors and curators allowed access to collections under their care, and others, including C. V. Covell in Kentucky and E. M. Shull in Indiana, quickly responded to requests for data. I also thank F. H. Rindge and Mary Genett, American Museum of Natural History, for searching Beutenmüller's files, and the late Alan Hayes for specimen photographs and label data in the British Museum (Natural History).

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CORRECTION OF A NAME IN THE *EPINOTIA VERTUMNANA* (ZELLER) SPECIES-GROUP (TORTRICIDAE)

In a revision of the *Epinotia vertumnana* (Zeller) species-group (Brown, R. L. 1986, J. Lepid. Soc. 40:327–346), *Paedisca celtisana* Riley (1881 [1882]) was transferred from synonymy with *Paedisca vertumnana* Zeller (1875) to synonymy with *Proteopteryx laracana* Kearfott (1907), with the latter name listed as the senior synonym. However, *Epinotia celtisana* (Riley) is the valid name by priority, and *Epinotia laracana* (Kearfott) becomes a junior synonym.

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TECHNICAL COMMENTS

LOGIC AND PHYLOGENY: A CRITIQUE OF SCOTT'S PHYLOGENIES TO THE BUTTERFLIES AND MACROLEPIDOPTERA

J. A. Scott (1985, J. Res. Lepid. 23:241–281; 1986, J. Res. Lepid. 25:30–38) proposed phylogenies to the Macrolepidoptera superfamilies (Fig. 1) and the butterfly families (Fig. 3, in part). Although he presented an impressive amount of data on comparative morphology and behavior, in many cases these data do not support his phylogenies. Because nonsystematists might easily overlook this problem among the pages of morphological detail, I present one example from each paper showing that his data are inconsistent with his results.

MACROLEPIDOPTERA

Ability to hear the ultrasounds produced by bats and other predators evolved at least three times in moths (Sales, G. & D. Pye 1974, Ultrasonic communication by animals, Chapman & Hall, London, 281 pp.). The Geometroidea and Pyraloidea possess an abdominal tympanum, the Noctuoidea a thoracic tympanum, and the Choerocampinae (Sphingidae) a tympanum on the head (labial palps). Scott (1985, above) proposed that the Noctuoidea, Bombycoidea, Sphingoidea, and butterflies form a monophyletic group. His evidence was that the geometroid abdominal tympanum evolved into a thoracic tympanum in the ancestor of these taxa (point T in Fig. 1). As he stated, "The tympana moved to the metathorax."

The noctuoid-to-butterfly grouping is not supported by the data. The bombycoids, sphingoids, and butterflies lack the thoracic tympanum. Scott's assumption that the abdominal geometroid tympanum is homologous with the thoracic noctuoid one is contradicted by the morphology and physiology of these structures (Forbes, W. T. M. 1916, Psyche 23:183–192; Richards, A. G. 1932, Entomol. Am. 13:1–43; Kiriakoff, S. G. 1952, Rev. Fr. Lepid. Fasc. 11–12:6 pp.; Maes, K. 1985, Nota Lepid. 8:341–350). No other characters support Scott's noctuoid-to-butterfly grouping. A slightly different, but simpler phylogeny (Fig. 2) reflects the lack of support for the noctuoid-to-butterfly grouping and requires only one evolutionary change as opposed to two (gain and loss of the thoracic tympanum) in Fig. 1.

BUTTERFLIES

There are three major types of male forelegs among the butterflies (Bates, H. W. 1861, J. Entomol. 1:218–245; Ford, E. B. 1945, Butterflies, the new naturalist, Collins, London, 368 pp.; Jander, U. 1966, Z. Tierpsychol. 23:799–844; Robbins, R. K. 1987, J. Lepid. Soc. 40:138–157).

TYPE I (Hesperiidae, Papilionidae, Pieridae). Foretarsi five-segmented with "spines," sensilla, and pretarsal claws. Forelegs used for walking and cleaning the antennae.

TYPE II (Lycaenidae *sensu* Eliot, J. N. 1973, Bull. Brit. Mus. (Nat. Hist.) Entomol. 28: 371–505, including the Curetinae). Foretarsi fused into one segment, retain "spines" and sensilla, but not pretarsal claws. Forelegs used for walking but not for cleaning the antennae.

TYPE III (Riodininae, Libytheidae, Nymphalidae *sensu* Ehrlich, P. R. 1958, Univ. Kans. Sci. Bull. 39:305–370). Foretarsi partially or wholly fused, covered dorsally and ventrally with long scales (the "brush foot"), devoid of "spines," sensilla, and pretarsal claws, and greatly reduced in size. Forelegs not used for walking or cleaning the antennae.

There are some exceptions to this summary (Type III forelegs occasionally have one or two "spines" or sensilla, some male lycaenids have a segmented and clawed foretarsus), but they are irrelevant to my argument.

Scott (1985, above) stated that the ancestor of the Lycaenidae-Libytheidae-Nymphalidae
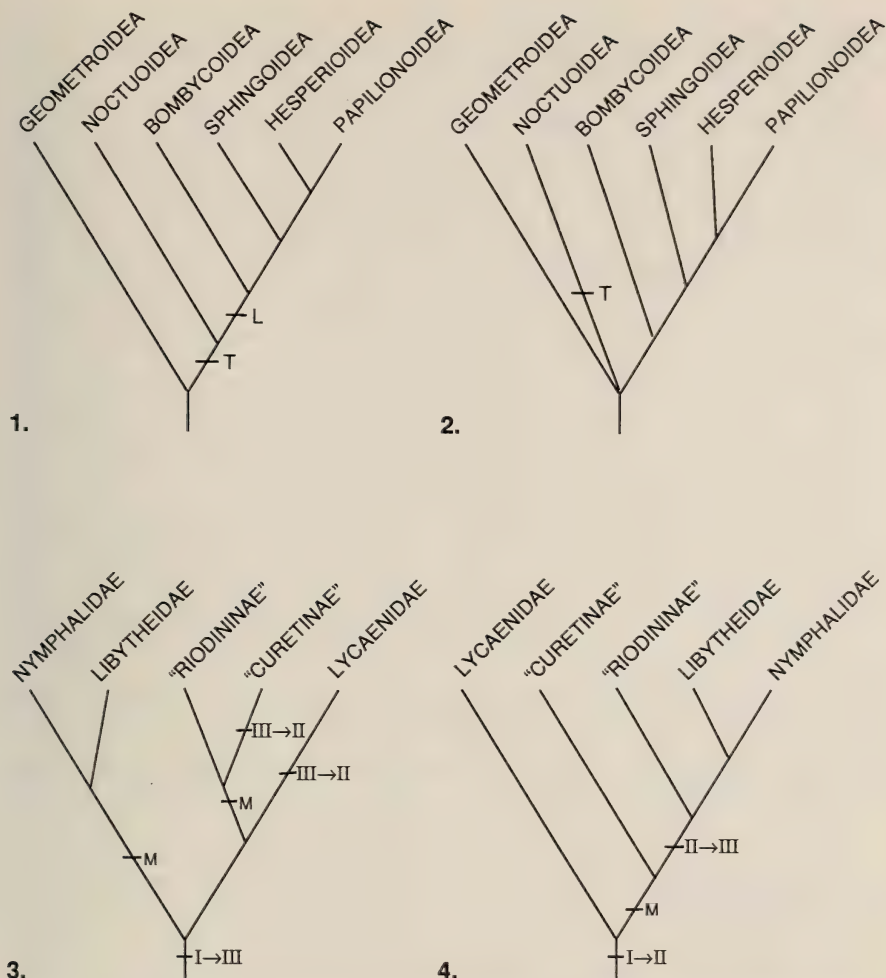
FIGS. 1–4. 1, 2. Phylogeny to the Macrolepidoptera. The thoracic tympanum evolved at point T, but was lost at point L. **1,** Scott's phylogeny requiring two evolutionary steps; **2,** An alternate phylogeny requiring one change. 3, 4. Phylogeny to the butterfly "families." Pupal midleg touching the eye evolved at point M. Evolution from one male foreleg type to another is represented by Roman numerals. The Styginae are omitted because of controversy over their male foreleg morphology (Forbes, W. T. M. 1960, Lepidoptera of New York and neighboring states, New York State College of Agriculture, Ithaca, 188 pp.); **3,** Scott's phylogeny requiring five evolutionary steps; **4,** An alternate phylogeny requiring three evolutionary steps.

had a small leg that could not clean the antennae. Since Type III forelegs are the only ones that are significantly reduced in size, Scott's statement implies that butterfly male forelegs evolved from Type I to Type III (in the lycaenid-nymphalid ancestor) to Type II (I-III-II hypothesis). This hypothesis, however, is less parsimonious than a I-II-III

proposal in Bates (above). The I-II-III hypothesis requires foreleg walking to be lost once (change from Type II to III) while the I-III-II hypothesis requires foreleg walking to be lost (change from I to III) and regained (change from III to II).

Scott's I-III-II hypothesis is inconsistent with his phylogeny (Fig. 3). The I-III-II hypothesis requires the Type II foreleg to evolve twice, once on the lineage to the Lycaenidae and once to the Curetinae (Fig. 3). The I-II-III hypothesis, on the other hand, implies an alternate phylogeny (Fig. 4) on which each male foreleg type evolves only once.

Scott further supported his I-III-II hypothesis by noting that the pupae of Curetinae have the midleg touching the eye, as in Nymphalidae, but again, this information does not support his phylogeny. As background, the Curetinae possess a Type II male foreleg. Scott noted that the pupal midleg character state occurs in Curetinae, Libytheidae, and Nymphalidae, but it also occurs in Riodinidae (Chapman, T. A. 1895, Entomol. Rec. J. Var. 6:101–107, 125–131, 147–152). Scott's phylogeny requires this character state to evolve twice (marked M in Fig. 3) while only one character change is necessary on the alternate phylogeny (point M in Fig. 4).

Scott presented much information besides that on male forelegs, and his phylogeny (Fig. 3) may be better supported by these other characters than the alternate phylogeny (Fig. 4). The important point is not which phylogeny is "correct" but that Scott incorrectly supported his I-III-II hypothesis with male foreleg and pupal midleg characters. This finding casts doubt on the validity of his analyses in general.

Phylogenies are basic to classification and to interpreting evolutionary hypotheses, but rigorously analyzed characters and character state distributions are needed to infer phylogenies. Scott claims to use cladistic methods, but his analyses appear to be inconsistent with cladistic methodology (Lundberg, J. G. 1972, Sys. Zool. 21:398–413; Farris, J. S. 1983, Adv. Cladistics 2:7–36). The prodigious amount of information that Scott presented on macrolepidopteran morphology and behavior will contribute to phylogenetic inference and, in this respect, is a major contribution to lepidopterology. However, it does not strongly support his conclusions.

I gratefully acknowledge John Burns, Gerardo Lamas, Scott Miller, Michael Pogue, Alma Solis, and Susan Weller for reviewing this comment.

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LOGIC AND PHYLOGENY: REPLY TO R. K. ROBBINS

Robbins is correct in questioning the homology of the noctuoid tympanum with other tympana. About the only use of tympana is to help indicate that Geometroidea split off the Macrolepidoptera line before Noctuoidea, although its detailed structure may provide useful traits within each superfamily. A fourth origin of the tympanum may be indicated by the dorsal as well as the usual ventral abdominal tympanum in *Habrosyne* (Thyatiridae). Strong characters are used to devise branching schemes, and weak characters such as the tympanum are merely dragged along to wherever the strong characters place them. The position of Noctuoidea in J. A. Scott (1986, J. Res. Lepid. 25:30–38) merely minimizes the number of character changes in the overall Macrolepidoptera tree. Geometroidea and Noctuoidea seem the most primitive Macrolepidoptera because their larvae generally lack secondary setae and retain uniordinal crochets, their pupae retain the temporal cleavage line and the visible prothoracic femur, adults retain ocelli and the upper sector of the paracoxal sulcus, and, with Bombycoidea, adults retain the parepisternal rift and an areole. Geometroidea is at the base of the Macrolepidoptera tree because its abdominal tympanum may be phylogenetically related to the Pyraloidea abdominal tympanum, and

because its flat eggs are more primitive than upright Noctuoidea eggs. The position of Noctuoidea after Geometroidea is also assigned by default because the cluster Bombycoidea-Sphingoidea butterflies share five derived traits (16–20 of Scott, above) which place this cluster on its own branch. Therefore, even when we discard the Noctuoidea tympanum because it evolved independently, Noctuoidea will have to stay put until new evidence to the contrary appears. The possible origin of Bombycoidea-Sphingoidea at the X of my Fig. 1 before Noctuoidea of Robbins' fig. 1 is equivalent to moving Noctuoidea to between Sphingoidea and Hesperioidea on Robbins' fig. 1, so I also was uncertain about the position of Noctuoidea. Currently, only these statements seem clear within Macrolepidoptera: 1) Geometroidea is the most primitive and Noctuoidea is next; 2) Bombycoidea and Sphingoidea are closely related; and 3) Hesperioidea-Papilionoidea are on their own branch. What is needed are new characters, which readers will hopefully provide.

Robbins' fig. 2 is improbable because we know that in nearly all cases two rather than three species evolve at one time, so a three-branch split is improbable on a phylogeny. Even if a three-branch split occurred during species-level evolution, the subsequent great animal extinction rate (estimated at 99%) would make the survival of all three taxa to the present exceedingly unlikely. Some authors draw as many as half a dozen lines branching from one point, but this merely reflects their uncertainty.

Among butterflies, the varying degrees of degeneration of the foreleg, especially the male foreleg, are weak traits that merely follow the strong traits when branching sequences are devised. I (below, pp. 256, 266) did not state that forelegs evolved from type I to III to II, only that the ancestor of Nymphalidae-Libytheidae-Lycaenidae had small forelegs, so that antennal cleaning by the middle leg evolved. Modifications of the foreleg such as tarsal fusion, claw loss, and scale elongation, or reversals of these states, apparently came later and proceeded differently in the various taxa. Libytheinae-Nymphalidae and Lycaenidae contain many groups with small forelegs, and they both clean the antenna with the middle leg; the logic that a small foreleg forced a switch from foreleg to middle leg cleaning seems inescapable. But just how small the ancestral foreleg was is not clear. Robbins assumes that it was his type III. Libytheinae was the first lineage to evolve from the nymphalid line, and its male foreleg is about one-half normal size while the female foreleg is about two-thirds normal size; even such a minimal reduction, occurring mainly in one sex, would have been enough to cause a shift to the middle leg. Or, a fusion of tarsal segments or loss of tarsal claws could have eliminated the ability of the leg to curve over the antenna shaft, reducing its utility in cleaning and causing the shift. Or, could a mere reduction of body size to lycaenid dimensions, together with a less-than-linear reduction of antennal shaft thickness due to a need to retain shaft rigidity to support the club, have reduced the ability of the antenna to flex backward with a small enough radius to be cleaned by the foreleg? If true, this ancestor would have a small foreleg in absolute dimensions, but a normal foreleg relative to the small middle and hind legs. One can classify the forelegs in various ways, many of which do not fit Robbins' I-II-III system, which is too simple and unnatural. For instance, Riodininae and Curetinae both have the male foreleg coxa extending spinelike below the articulation with the trochanter, an odd trait that may show their phylogenetic relatedness (both share other traits cited by Scott, J. A. 1985, J. Res. Lepid. 23:241–281, including the middle leg touching the pupal eye, noticed in Riodininae by Chapman, T. A. 1895, Entomol. Rec. J. Var. 6:129). Many Lycaeninae have a segmented and clawed male tarsus (Eliot, J. N. 1973, Bull. Brit. Mus. [Nat. Hist.] Entomol. 28:373–505), contrary to Robbins' type II; Eliot (pp. 394–395) argues that some groups have reacquired segmented and clawed male forelegs. Nymphalidae also show varying degrees of modifications of the tarsus (Ehrlich, P. R. 1958, Univ. Kans. Sci. Bull. 39:305–379). It seems difficult to avoid the conclusion that there have been many independent modifications of male foreleg details, including reversals. Robbins is correct that a I-II-III sequence would be more parsimonious; however, parsimony of entire phylogenetic trees overrides parsimony within a single character, and trees forced to obey Robbins' I-II-III sequence would require numerous added character changes in the tree because this sequence requires Nymphalinae to be evolved from the Lycaeninae-Curetinae ancestor.

Robbins' fig. 4 is impossible because of the massive number of shared derived traits of

Lycaenidae (including Riodininae, Miletinae, Curetinae, Lycaeninae), some newly dis-
covered on the first stage larva by D. M. Wright. Fully 28 strong shared derived traits
now define Lycaenidae, and seven shared derived traits define Nymphalidae (including
Libytheinae) (Scott above, and Scott, J. A. & D. M. Wright, Butterfly phylogeny and
fossils, *in* Kudrna, Otakar (ed.), Butterflies of Europe, Vol. 2, Aula-Verlag, Wiesbaden,
in press). Just as the principle of parsimony has its final judgment on entire trees rather
than single characters, phylogenies must be based on numerous characters—the more the
better—and not on single characters. There will always be characters that are weak or
difficult to interpret, or that show reversals, and even when worthless characters are
discarded the remaining characters will not be of equal value; robust characters should
be given greater weight. The shift to middle leg antenna cleaning is a strong character,
but the detailed modifications of the male foreleg represent weak characters. The evo-
lutionary history of weak characters is best determined by devising a phylogenetic tree
using all characters (weighting the strong characters more heavily) and then using that
tree to determine what happened to the weak traits. Using this method, the ancestral
nymphalid-lycaenid foreleg may have shrunk to Libytheinae size, then later in Nym-
phalidae the male and female foreleg shrank further, while in Lycaenidae the Libytheinae-
type foreleg changed to a feather-duster type male foreleg in Riodininae, and in Ly-
caeninae the foreleg became larger again, etc.; but all we know for certain is that the
ancestral nymphalid-lycaenid foreleg was small in at least one sex.

The character of the pupal middle leg touching the eye would have to evolve only
once on my phylogeny (in the ancestor of Nymphalidae-Lycaenidae) contrary to Robbins,
and would have to be lost only once (in the ancestor of Lycaeninae, because Riodininae
also have the trait).

It is good to question phylogenies, but one should not waste much time on weak
characters; better to look for new characters, because the more one looks at a group of
organisms, the more characters one finds. In most groups one can quintuple the known
list of characters with hard work using morphology and behavior of all life stages.

My two papers are "cladistic" because they use the main two principles of cladistics,
that a branch must be defined using shared derived traits, and that each branch must be
monophyletic. Of numerous rules in cladistic variants, only those two rules are really
necessary. It is also important to list all the character changes that must have occurred
on the branches of the chosen tree to produce the character states observed in the living
taxa; thus some weak characters are inevitably listed even though not given much weight
in choosing the branching sequence of the chosen tree.

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OBITUARY

André Blanchard (1896–1986)

At 0730, 17 October 1986, the international lepidopterist community lost one of its most dedicated and capable amateurs. André Blanchard had been confined to his home at 3023 Underwood, Houston, Texas, for several years due to fibrosis of the lungs. Failing health made it necessary to discontinue in mid-November 1977 his most successful and rewarding field work on the Lepidoptera. Although confined, his interest in Lepidoptera did not diminish. Instead, he began studying in more detail the material at hand which resulted in the publication of 34 papers. In a personal communication dated 19 August 1985 referring to a paper in preparation on *Chlamydastis,* he remarked: "This paper will almost certainly be my last". It was. A year later on 20 August 1986 he fell in his home, fracturing a hip. He underwent surgery to repair the fracture, but after two months' hospitalization the fracture did not heal, and due to general infection he passed away. His wife May Elise was at his bedside throughout the long hospital stay. Interment was in Calvary Cemetery, Houston, Texas, as he wished.

André was born 11 June 1896 at Marennes (Charente Maritime), France, the youngest of two sons and a daughter (Suzanne) born to François Issac Blanchard and Marie Voyer. His father was affiliated with a banking facility. His older brother René was killed in action in World War I. In 1914 at age 18, through competitive examination, André was admitted to the Ecole Navale (French Naval Academy). Following graduation in 1917 he served with the French Navy until 1929.

While on active duty during World War I, André served on a battleship in the Mediterranean, and a destroyer in the North Sea. During his last war year (1918), André was a seaplane pilot escorting ship convoys from Brest (Brittany) to Penzance (Cornwall). Early in 1919, following termination of the war, André was dispatched to New York to join the French battlecruiser Marseillaise. This marked his first visit to the New World which he found most enjoyable. In mid-1919 he returned to France and joined a group working under the leadership of Paul Langevin, a physicist doing research on the newly invented sonar. In April 1921, at his own request, André spent the next 12 months at Ecole Supérieure de Radiotechnique in Paris where he became a radio engineer. The remainder of his military career was at the Laboratoire du Centre d'Etudes de la Marine in Toulon, France. Here he not only taught radio but wrote the text which was later used at the Naval Academy. For two years (October 1927 to October 1929) he was commander of the 900-ton ship Les Eparges, especially equipped as the floating laboratory of the Centre d'Etudes.

Military honors received included the Croix de Guerre, 20 May 1917; Chevalier of the Legion of Honor, 8 January 1927; Officer of the Legion of Honor, 31 December 1950.

In October 1929, Michelin Tire Company, Clermont-Ferrand, France, made André an offer which he could not refuse. He was placed in charge of the Company's physics laboratory where he directed significant research on rubber, carbon black, heat-treatment of steel, and steel wire drawing. At the outbreak of World War II, André became head of the department that produced the new "metallic tire". Thinking the patents might be sold to American tire companies in connection with the war effort, André was one of a delegation of five who left France in January 1941 for the United States to present the Michelin proposal. The deal failed and the delegation was denied exit visas until the end of the war. Not willing to remain inactive due to circumstances beyond his control, André went to work for the United States War Department translating from English to French military manuals ranging from Aerial Celestial Navigation to Optical Rangefinders. Meantime in France, his wife and two daughters were being well cared for by Michelin. In October 1943, Schlumberger Well Services became aware of André's availability, and hired him for the duration. After the armistice in Europe, André returned to France, his family, and Michelin. However, an overriding bond had been developed between André and Schlumberger; as a result, he returned to the United States in August 1946 with his family. Here he was again employed by Schlumberger, first as Manager of Engineering, later as Vice President of Engineering, and finally as Vice President of Research and

André Blanchard

Development. He retired 30 June 1961 at age 65, but remained a paid consultant with Schlumberger for four more years.

André's family life began 22 April 1921 when he married Marguerite Normand at Loches, France. Born to this marriage were two daughters, Simone Blanchard Gérard, and Michelle Blanchard Gaymard. In 1958, following a long illness, Marguerite died, and on 9 May 1959 André and May Elise Moraud of Houston were married. No children were born to this union. André is survived by his devoted wife, May Elise, two daughters (Simone and Michelle), eight grandchildren and eight great-grandchildren.

André's avocation as a lepidopterist began in about 1925 when his wife, Marguerite, suggested that they should have a hobby. After thoughtful consideration they chose butterfly collecting. To house the European butterflies they would catch, some 30 glass-top specimen cases with cork pinning bottoms were manufactured. Collections were made as time permitted during the remaining years they spent in Europe. Unfortunately, there

was little time in his busy schedule to properly curate the collection, and it was virtually destroyed by dermestids. Nevertheless, when André and his family moved to the United States, the specimen cases came along and served as initial storage for his collection of Texas specimens.

André joined the Lepidopterists' Society in 1957. His primary interest at that time was butterflies. It was a paper of mine in 1959 (J. Lepid. Soc. 13:221–228) that brought us together. On 30 October 1960 he wrote, "I have been myself hoping for two to three years to find the foodplant of *Phyciodes texana*. I have not been as lucky as you but I feel very definitely that one more plant should be added to your list of four—*Dicliptera brachiata*." On 26 November 1960 we met and together in Memorial Park (Houston, Texas) learned that indeed *Dicliptera brachiata* is used in nature by this species. That meeting marked the beginning of a most enjoyable friendship between our two families for more than 25 years. During one of our early meetings, André remarked: "There is no need for both of us to work on the butterflies of Texas, I'm going to work on the moths."

Upon retirement André began collecting both seriously and enthusiastically. At first he used bait traps, UV and mercury-vapor lights set on a white bedsheet. In 1962 the late Perry A. Glick showed André a light trap used by the U.S. Department of Agriculture for sampling economic nocturnal insects. On 24 February 1963 he visited Joe P. Hollingsworth, College Station, Texas, who was working on a new model light trap for the Department. Measurements were taken and a sketch made of the new model; four days later André had his light trap. After putting the trap into use he learned that during certain times of the season many Coleoptera would come to the light, and because beetles are so slow to die they would virtually destroy Lepidoptera in the trap. This problem was essentially solved by a novel modification he made which separated most Coleoptera from Lepidoptera.

Now, using three modified light traps, André started sampling nocturnal Lepidoptera statewide. Field trips were planned following the new moon which provided the longest periods of darkness. During the 16 years that followed many field trips were made throughout Texas resulting in the first statewide survey of noneconomic Lepidoptera (moths). May Elise accompanied him on every field trip, helped set up the traps in the evening, and helped pick them up early the following morning. After sorting the catch, specimens to be kept were placed in a relaxer, later pinned and spread in the field. Spread specimens were placed immediately in a dryer. Thus, except for the last catch of the trip, specimens taken were ready to be labeled and placed in the collection upon returning home. Many of the unwanted specimens were papered by May Elise to be given to correspondents or to museums.

In early 1962 André was already thinking of preparing a checklist for Texas moths. To this end, a card file of species recorded from the State was initiated. At the same time additional specimen cases were being made to house the eventual collection of some 60,000 spread specimens. He also began learning the technique of dissecting genitalia. A special collection of literature was accumulated. He was already expert at photography.

Almost from the beginning of his intensive work on the moths of Texas, it became apparent that certain families and genera were in need of revision. As undescribed species accumulated this situation became a problem. He then began seeking help and advice from professional lepidopterists. Both he and his work were greatly respected within professional circles, thus the help needed came easy, although much too slow at times to please him. With the publication in 1983 of the *Check List of the Lepidoptera of America North of Mexico*, the way was cleared for at least a tentative State list but it came too late. Failing health demanded that he limit his activities to describing some of the new species he had collected.

On 15 August 1977, André informed me that Edward C. Knudson, M.D., another amateur Texas lepidopterist, had visited him the day before, bringing along a box of moths for determination. He had been greatly impressed both by Knudson and the specimens brought for examination. As it turned out, this was the beginning of a continuing and deepening friendship between them. They worked together perfectly, and their manuscript production speaks for itself. Knudson will continue the statewide survey; he has prepared a tentative checklist representing more than 3000 moth taxa.

André's lepidopterological affiliations included: American Museum of Natural History (life member); The Lepidopterists' Society, regular and sustaining member (1957–86), member-at-large of the Executive Council (1971–73), president (1975–his presidential address, J. Lepid. Soc. 30:1–4); The Lepidoptera Research Foundation (charter and regular member to July 1985); The Entomological Society of Washington (regular member 1968–86); Southern Lepidopterists' Society (regular member 1985–86) from which he received the John Abbot Award 19 October 1985 for significant research on the Lepidoptera of Texas.

Currently, fellow lepidopterists have described eighteen species honoring André and May Elise. Doubtless others will follow. A list of these patronyms together with other pertinent data is given in a later section.

André prearranged disposition of his specimens, and "tools" for collecting and studying Lepidoptera. His primary collection of Texas insects went to the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C. Based on an inventory by that institution (J. Lepid. Soc. 39:235–236), the collection totaled 76,852 specimens of which 16,305 were Coleoptera and 60,233 Lepidoptera. The latter, largest single accumulation of Lepidoptera ever made from Texas, included 82 holotypes, 700 paratypes, and 4600 microslides, mostly of genitalia. Both micro- and macro-Lepidoptera are represented with more than 65 percent in four family groups: Noctuidae 18,500+, Pyraloidea 9000+, Geometridae ca. 8000 and Tortricoidea ca. 4000 specimens. Frederick H. Rindge, American Museum of Natural History (AMNH), New York, New York, advised (21 November 1986) that from 1958 through 1976 the AMNH received from Blanchard 16,500 specimens of Texas Lepidoptera, and before this, about 1943, a number of specimens from the islands of Martinique and Guadaloupe were donated by him. Of course many other institutions and individuals received small numbers of specimens, including paratypes, which André had collected or described.

André's "tools" for studying Lepidoptera included library material, optical equipment, photographic equipment, a card file of species taken or recorded from Texas, correspondence dealing with Lepidoptera, specially designed spreading boards, UV light traps, and specimen cases. The library material was given to Rice University, Edward C. Knudson, and Roy O. Kendall; the optical equipment and spreading boards to Knudson and Kendall; specimen cases (31) brought from France, to Kendall, other cases to USNM with the primary collection; all remaining "tools" to Knudson.

Finally, on behalf of André's friends, I paraphrase in part a classical eulogy: Rest, dear friend, lie down for an aeon or two until the Master of all good Lepidopterists shall put you to collecting anew. You will long be remembered by those of us who knew you, and your scientific contributions to the advancement of lepidopterology will live forever, but we think you knew that.

PATRONYMS

Lepidopterists have described eighteen species honoring André and May Elise Blanchard. It seems appropriate that the list include those named for May Elise as well as André because they worked together in the field as a team. Still other patronyms honoring Blanchard will probably appear. The list of patronyms should be seen as a tribute to Blanchard for his significant contribution to the scientific advancement of lepidopterology, especially in Texas. No other individual has contributed so much toward a better understanding of the Lepidoptera of Texas.

Gelechiidae

Dichomeris blanchardorum R. W. Hodges 1986. Gelechioidea, Gelechiidae (in part), *in* Dominick, R. B., et al., *The Moths of America North of Mexico*, Fasc. 7.1:43. Type Locality (TL): Texas, Cameron Co., Laguna Atascosa [National Wildlife Refuge]. Holotype ♂ in USNM.

Geometridae

Plataea blanchardaria E. C. Knudson 1986. Proc. Entomol. Soc. Wash. 88:351–353. TL: Texas, Duval Co., 13 km W of Premont. Holotype ♂, 30 June 1985, in USNM.

Sicyopsis blanchardata D. C. Ferguson 1983. J. Lepid. Soc. 37:24–28. TL: Texas, Culberson Co., Guadalupe Mountains [National Park], Smith Canyon, 1753 m. Holotype ♂, 22 May 1973, in USNM.

Stenoporpia blanchardi F. H. Rindge 1968. Bull. Am. Mus. Nat. Hist. 140:65–134 (116, 117). TL: Texas, Brewster Co., Big Bend National Park, Basin. Holotype ♂, 9 April 1967, allotype-topotype ♀, 4 October 1967, both in AMNH.

Glyphipterigidae

Drymoana blanchardi J. B. Heppner 1985. *The Sedge Moths of North America* (Handbook No. 1). Flora & Fauna Publ., Gainesville, Florida, x + 254 pp. (49–53). TL: Texas, Jackson Co., Deutschburg [nr. Carancahua Creek, S of Francitas]. Holotype ♂, 7 October 1974, in USNM.

Lasiocampidae

Apotolype blanchardi J. G. Franclemont 1973. Mimallonoidea, Bombycoidea (in part), *in* Dominick, R. B., et al., *The Moths of America North of Mexico*, Fasc. 20.1:48, 49. TL: Texas, Cameron Co., Brownsville. Holotype ♂, 7 November 1969, in USNM.

Tolype mayelisae J. G. Franclemont 1973. Mimallonoidea, Bombycoidea (in part), *in* Dominick, R. B., et al., *The Moths of America North of Mexico*, Fasc. 20.1:37, 38. TL: Texas, Brewster Co., Alpine. Holotype ♀, 2 October 1963, in USNM.

Noctuidae

Basilodes [*Stiria*] *blanchardi* C. L. Hogue 1966. J. Res. Lepid. 4:275–280. TL: New Mexico, Eddy Co., Carlsbad Caverns National Park. Holotype ♂, 17 September 1963, in Los Angeles County Museum of Natural History.

Grotella blanchardi R. R. McElvare 1966. J. Lepid. Soc. 20:91, 92. TL: New Mexico, Eddy Co., White City. Holotype ♂, 17 September 1963, in USNM.

Opsigalea blanchardi E. L. Todd 1966. Proc. Entomol. Soc. Wash. 68:149–151. TL: Texas, Brewster Co., Alpine. Holotype ♂, 9 September 1963, in USNM.

Pyralidae

Acrobasis blanchardorum H. H. Neunzig 1973. Proc. Entomol. Soc. Wash. 75:165–169. TL: Texas, Culberson Co., Sierra Diablo Wildlife Management Area, 1829 m. Holotype ♂, 5 June 1969, in USNM (type no. 72179).

Homosassa blanchardi J. C. Shaffer 1976. Proc. Entomol. Soc. Wash. 78:431–434. TL: Texas, Harris Co., Houston. Holotype ♂, 5 June 1967, in USNM (type no. 72179).

Mojaviodes blanchardae E. G. Munroe 1972. Pyraloidea (in part), *in* Dominick, R. B., et al., *The Moths of America North of Mexico*, Fasc. 13.1B:188. TL: Texas, Presidio Co., Shafter. Holotype ♂, 9 September 1969, in USNM.

Pyrausta andrei E. G. Munroe 1976. Pyraloidea (in part), *in* Dominick, R. B., et al., *The Moths of America North of Mexico*, Fasc. 13.2B:127, 128. TL: Texas, Brewster Co., Big Bend National Park, Green Gulch. Holotype ♀, 28 March 1971, in USNM.

Scoparia blanchardi E. G. Munroe 1972. Pyraloidea (in part), *in* Dominick, R. B., et al., *The Moths of America North of Mexico*, Fasc. 13.1A:39, 40. TL: Texas, Jeff Davis Co., Davis Mountains, Mount Locke. Holotype ♂, 6 September 1969, in USNM.

Saturniidae

Sphingicampa blanchardi D. C. Ferguson 1971. Bombycoidea (Saturniidae), *in* Dominick, R. B., et al., *The Moths of America North of Mexico*, Fasc. 20.2:47–50. TL: Texas, Cameron Co., Brownsville, Esperanza Ranch [now city housing]. Holotype ♂, no date, in USNM (type no. 71494).

Sphingidae

Amplypterus [*Adhemarius*] *blanchardorum* R. W. Hodges 1985. Proc. Entomol. Soc. Wash. 87:323–328. TL: Texas, Brewster Co., Big Bend National Park, Chisos Mountains, Panther Pass, 1829 m. Holotype ♂, 4 June 1973, in USNM.

Tortricidae

Rhyacionia blanchardi W. E. Miller 1978 *in* Powell, J. A. & W. E. Miller, U. S. Dept. Agric. Handbook 514, 51 pp. (19–21). TL: Texas, Montgomery Co., Conroe. Holotype ♂, 10 March 1968, allotype-topotype ♀, 9 March 1971, both in USNM.

BIBLIOGRAPHY

. At the time of his death two additional papers had been drafted in which Blanchard was junior author: 1) With R. W. Poole, describing two new genera and two new species of Noctuidae from Texas; and with J. G. Franclemont on the noctuid genus *Protoperigea*.

The bibliography is divided into two sections, one dealing with European Lepidoptera (I–VIII), the other with North American Lepidoptera (1–59). Species treated in the latter are indexed under two headings: New Genera and Species, and Rare and Interesting Records. In each instance the new genera and species are arranged alphabetically and keyed to the numbered paper in the bibliography.

Early Publications on Lepidoptera of France

I. 1937. *Thaïs rumina* dans la vallée de la Jonte. L'Amateur de Papillons 8:252.

II. 1937. *Parnassius mnemosyne* dans le Puy-de-Dôme. L'Amateur de Papillons 8: 252, 253.

III. 1938. Un arc-en-ciel d'ecailles de papillons. Rev. Franç. Lépid. 9:11–14.

IV. 1938. L'Elevage de *Macrothylacea rubi* Linné. Rev. Franç. Lépid. 9:57–61.

V. 1938. Capture en Auvergne d'*Heodes amphidamas* Esp. (Lycaenidae). Rev. Franç. Lépid. 9:147–148.

VI. 1940. Contribution a la connaissance de la faune des Lépidoptères du Puy-de-Dôme. Rev. Sci. Nat. d'Auvergne 6:18–20.

VII. 1940. Faune des Lepidopteres d'Auvergne. Rev. Sci. Nat. d'Auvergne (N.S.) 6(1–2):18–20.

VIII. 1940. Observations sur quelques lépidoptères d'Auvergne. Rev. Sci. Nat. d'Auvergne (N.S.) 6(3–4):81–88.

Publications on Lepidoptera of North America

1. 1963. Contribution to the life history of *Schoenobius maximellus* (Pyralididae). J. Lepid. Soc. 17:234–235.

2. 1964. The food plants of *Syssphinx heiligbrodti* (Saturniidae) in Texas. J. Lepid. Soc. 18:42.

3. 1966. A new species of *Glaucina* (Geometridae) from Texas. J. Lepid. Soc. 22:247–250.

4. 1968. New moths from Texas (Noctuidae, Tortricidae). J. Lepid. Soc. 22:133–145.

5. 1969. A gynandromorphic *Phaeoura mexicanaria* (Geometridae). J. Lepid. Soc. 23: 274–275.

6. 1970. Observations on some Phycitinae (Pyralidae) of Texas with descriptions of two new species. J. Lepid. Soc. 24:249–255.

7. 1971. Notes on three species of *Heterocampa* Doubleday with description of a new species. (Lepidoptera: Notodontidae). Proc. Entomol. Soc. Wash. 73:249–254.

8. 1971. A new species in the genus *Ursia* Barnes & McDunnough (Lepidoptera: Notodontidae). Proc. Entomol. Soc. Wash. 73: 303–305.

9. 1972. More new moths from Texas (Noctuidae). J. Lepid. Soc. 26:56–63.

10. 1972. A new species of the genus *Pyromorpha* Herrich-Schaeffer (Pyromorphidae). J. Lepid. Soc. 26:79–82.

11. 1973. Record and illustration of some interesting moths flying in Texas (Sphingidae, Ctenuchidae, Noctuidae, Notodontidae, Geometridae, Pyralidae, Cossidae). J. Lepid. Soc. 27:103–109.

12. 1973. A new species of the genus *Glenoides* McDunnough (Geometridae). J. Lepid. Soc. 27:141–143.

13. 1973. Two new species of Phycitinae from Texas, with description of two new genera (Pyralidae). J. Lepid. Soc. 27:219–225.

14. 1973. *Erratum.* J. Lepid. Soc. 27:278. (Corrects a name in J. Lepid. Soc. 24:249–255; *Dioryctria auranticella* (Grote) should be *Dioryctria rossi* Munroe.)

15. 1975. A new phycitine genus and species (Pyraloidea). J. Lepid. Soc. 29:95–97.

16. 1975. A new schoenobine genus and species (Pyraloidea). J. Lepid. Soc. 29:98–101.

17. *Rostrolaetilia*—A new North American genus of the subfamily Phycitinae, with descriptions of seven new species (Pyralidae). J. Lepid. Soc. 29:131–150.

18. 1976. Presidential address 1975—To my fellow amateurs. J. Lepid. Soc. 30:1–4.

19. 1976. The genus *Copablepharon* in Texas, with description of three new species (Noctuidae). J. Lepid. Soc. 30:116–120.

20. 1976. A new species of the genus *Bertella* Barnes & McDunnough (Pyralidae). J. Lepid. Soc. 30:211–213.

21. 1976. Two new species of phycitine moths with description of a new genus (Pyralidae). J. Lepid. Soc. 30:284–288.

22. 1976. *Oenobotys texanalis.* (With Eugene Munroe sr. author.) Pyraloidea (in part), *in* Dominick, R. B., et al., *The Moths of America North of Mexico,* Fasc. 13.2A:18–19.

23. 1978. *Atopothoures* A. Blanchard a synonym of *Goya* Ragonot (Pyralidae). J. Lepid. Soc. 32:55–56.

24. 1978. The status of *Ollia parvella* Dyar: Redescription in a new genus (Pyralidae). J. Lepid. Soc. 32:103–106.

25. 1979. New status for *Epiblema minutana* (Kearfott) and new species of *Epiblema* Hübner and *Sonia* Heinrich (Tortricidae). J. Lepid. Soc. 33:179–188.

26. 1980. Five new species of the tribe Eucosmini (Tortricidae). J. Lepid. Soc. 33:209–215.

27. 1981. A new species of the genus *Peoria* Ragonot (Pyralidae). J. Lepid. Soc. 34:338–339.

28. 1981. *Charadra ingenus* Smith in West Texas (Lepidoptera: Noctuidae: Pantheinae). (With J. G. Franclemont jr. author.) Proc. Entomol. Soc. Wash. 83:797–798.

29. 1982. A new species of *Zale* Hübner from Texas and New Mexico (Lepidoptera: Noctuidae: Catocalinae). (With J. G. Franclemont jr. author.) Proc. Entomol. Soc. Wash. 84:134–137.

30. 1982. Two new species of the tribe Eucosmini (Tortricidae). (With E. C. Knudson jr. author.) J. Lepid. Soc. 35:169–172.

31. 1982. Two new species of *Eucosma* Hübner (Tortricidae) from Texas. (With E. C. Knudson jr. author.) J. Lepid. Soc. 35:173–178.

32. 1982. A new species of *Ozamia* Ragonot (Pyralidae) from Texas. (With E. C. Knudson jr. author.) J. Lepid. Soc. 35:233–235.

33. 1982. *Marilopteryx carancahua,* a new genus and new species from East Texas (Lepidoptera: Noctuidae: Hadeninae). (With J. G. Franclemont jr. author.) Proc. Entomol. Soc. Wash. 84:270–276.

34. 1982. A new species of *Symmetrischema* Povolny (Lepidoptera: Gelechiidae) from Texas. (With E. C. Knudson jr. author.) Proc. Entomol. Soc. Wash. 84:628–631.

35. 1983. Two new species of Pyralidae (Lepidoptera) from Texas. (With E. C. Knudson jr. author.) Proc. Entomol. Soc. Wash. 85:59–63.

36. 1983. A new species of *Dioryctria* Zeller (Lepidoptera: Pyralidae) from Texas. (With E. C. Knudson jr. author.) Proc. Entomol. Soc. Wash. 85:116–120.

37. 1983. A new species of *Gloanna* Nye (Lepidoptera: Noctuidae) from West Texas. (With E. C. Knudson jr. author.) Proc. Entomol. Soc. Wash. 85:174–176.

38. 1983. A new genus and species of Geometridae (Lepidoptera) from Big Bend National Park, Texas. (With D. C. Ferguson sr. and E. C. Knudson jr. authors.) Proc. Entomol. Soc. Wash. 85:552–556.

39. 1983. A new species of *Psorosina* Dyar (Lepidoptera: Pyralidae) from Texas. (With E. C. Knudson jr. author.) Proc. Entomol. Soc. Wash. 85:619–621.

40. 1983. Two new species of the tribe Eucosmini (Tortricidae) closely related to *Phaneta granulatana* (Kearfott). (With E. C. Knudson jr. author.) J. Lepid. Soc. 37:140–145.

41. 1983. New North American species of Eucosmini (Lepidoptera: Tortricidae). (With E. C. Knudson jr. author.) Proc. Entomol. Soc. Wash. 85:845–852.

42. 1984. A new species of *Hypomecis* Hübner (Lepidoptera: Geometridae) from Texas and Florida. (With E. C. Knudson jr. author.) Proc. Entomol. Soc. Wash. 86:291–294.

43. 1984. A new *Stibadium* from Texas and a redescription of *Striodes edentatus* (Grote) (Noctuidae: Lepidoptera). (With E. C. Knudson jr. author.) Proc. Entomol. Soc. Wash. 82:346–348.

44. 1984. Three new tortricids (Lepidoptera) from Texas. (With E. C. Knudson jr. author.) Proc. Entomol. Soc. Wash. 86:446–451.

45. 1984. A new species of *Tripudia* Grote (Lepidoptera: Noctuidae) from western Texas. (With E. C. Knudson jr. author.) Proc. Entomol. Soc. Wash. 86:639–642.

46. 1984. A new species of *Neodavisia* Barnes & McDunnough (Lepidoptera: Pyralidae) from southern Texas. (With D. C. Ferguson sr. and E. C. Knudson jr. authors.) Proc. Entomol. Soc. Wash. 86:769–772.

47. 1984. A revision of the genus *Aleptina* (Lepidoptera: Noctuidae). (With E. L. Todd sr. and R. W. Poole jr. authors.) Proc. Entomol. Soc. Wash. 86:951–960.

48. 1985. New species of Phycitinae (Lepidoptera: Pyralidae) from Texas, with description of a new genus. (With E. C. Knudson jr. author.) Proc. Entomol. Soc. Wash. 87:231–238.

49. 1985. A new species of *Bucculatrix* Zeller (Lepidoptera: Lyonetiidae) from Texas. (With E. C. Knudson jr. author.) Proc. Entomol. Soc. Wash. 87:371–374.

50. 1985. *Psychonoctua masoni* (Schaus), new combination (Lepidoptera: Cossidae: Zeuzerinae), redescription and first records from Texas and USA. (With E. C. Knudson jr. author.) Proc. Entomol. Soc. Wash. 87:426–431.

51. 1985. Two new Phycitinae (Lepidoptera: Pyralidae) from Texas and Alabama. (With E. C. Knudson jr. author.) Proc. Entomol. Soc. Wash. 87:475–479.

52. 1985. The *Eupithecia* (Lepidoptera: Geometridae) of Texas, with the description of a new species. (With E. C. Knudson jr. author.) Proc. Entomol. Soc. Wash. 87:662–674.

53. 1985. *Epiblema luctuosana* A. Blanchard, a homonym, is changed to *Epiblema luctuosissima,* new name. J. Lepid. Soc. 38:245.

54. 1985. *Ethmia angustalatella* Powell (Lepidoptera, Oecophoridae): Description of the female and first U.S. records. Proc. Entomol. Soc. Wash. 87:680–681.

55. 1985. Checklist of Lepidoptera of the Rob and Bessie Welder Wildlife Refuge near Sinton, Texas. (Blanchard et al.) Southwest. Entomol. 10:195–214.

56. 1985. New U.S. records and other interesting moths from Texas. (With E. C. Knudson jr. author.) J. Lepid. Soc. 39:1–8.

57. 1985. Two new species of *Hexorthodes* (Lepidoptera: Noctuidae) from Texas and Arizona. (With E. C. Knudson jr. author.) Proc. Entomol. Soc. Wash. 87:777–782.

58. 1986. Four new moths from Texas (Lepidoptera, Geometridae, Noctuidae). (With E. C. Knudson jr. author.) Proc. Entomol. Soc. Wash. 88:134–141.

59. 1986. A new *Chlamydastis* (Oecophoridae, Lepidoptera) from Texas. (With E. C. Knudson jr. author.) Proc. Entomol. Soc. Wash. 88:185–188.

NEW GENERA AND SPECIES

Items are arranged alphabetically and keyed to the bibliography.

Genera

Atopothoures [=*Goya* Ragonot 1888]   Pyralidae: Peoriinae   **15, 23**
Carectocultus   Pyralidae: Schoenobiinae   **16**
Glyphocystis   Pyralidae: Phycitinae   **13**
Pimodes   Pyralidae: Phycitinae   **21**
Pseudocabotia   Pyralidae: Phycitinae   **48**
Rostrolaetilia   Pyralidae: Phycitinae   **17**
Triozosneura   Pyralidae: Phycitinae   **13**
Welderella   Pyralidae: Phycitinae   **24**

Species

adusta, Euamiana   Noctuidae   58
    TL: Texas, Jeff Davis Co., Davis Mountains, Madera Canyon. Holotype (HT) ♂, 17 August 1984, in USNM.
albisericea [*albisericeum*], *Copablepharon*   Noctuidae   19
    TL: Texas, Hemphill Co., nr. Canadian, Gene Howe Wildlife Management Area. HT ♂, 27 September 1968, in USNM (type no. 73431).
anaimella, Meroptera   Pyralidae   48
    TL: Texas, Presidio Co., Shafter. HT ♂, 9 July 1969, in USNM.
apicigrammella, Melitara   Pyralidae   48
    TL: Texas, Terrell Co., Sanderson. HT ♂, 28 September 1980, in USNM.
arenella, Eoreuma   Pyralidae   35
    TL: Texas, [Kleberg Co.], Padre Island National Seashore. HT ♂, 19 July 1976, in USNM.
argutipunctana, Phaneta   Tortricidae   40
    TL: Texas, Hemphill Co., Canadian. HT ♂, 15 August 1971, in USNM.
atascosana, Eucosma   Tortricidae   26
    TL: Texas, Cameron Co., Laguna Atascosa National Wildlife Refuge. HT ♂, 22 November 1973, in USNM (type no. 75821).
atratella, Salebriaria   Pyralidae   51
    TL: Texas, Hunt Co., Lake Twakoni, Wind Point Park. HT ♂, 15 July 1984, in USNM.
auripurpura, Hydroecia   Noctuidae   4
    TL: Texas, [Brewster Co.], Big Bend National Park, Green Gulch, 1613 m. HT ♂, 11 October 1966, in USNM (type no. 68160).
balconiensis, Pseudocabotia   Pyralidae   48
    TL: Texas, Kerr Co., 10 miles west of Hunt. HT ♂, 4 September 1981, in USNM.
benitensis, Heterocampa   Notodontidae   7
    TL: Texas, Cameron Co., Brownsville. HT ♂, 8 August 1967, in USNM (type no. 64647).
bucurvata, Astalotesia   Geometridae   38
    TL: Texas, Brewster Co., Big Bend National Park, Chisos Basin. HT ♂, 29 March 1982, in USNM.
caelebs, Pyromorpha   Zygaenidae   10
    TL: Texas, Jeff Davis Co., Fort Davis, Hospital Canyon. HT ♂, 18 May 1971, in USNM (type no. 71981).
caesirufella, Dioryctria   Pyralidae   36
    TL: Texas, Kerr Co., Kerrville State Park. HT ♂, 19 August 1980, in USNM.
caesium, Stibadium   Noctuidae   43
    TL: Texas, Cameron Co., south Padre Island. HT ♂, 24 October 1982, in USNM.
callaisata, Paramiana   Noctuidae   9
    TL: [Texas, Culberson Co.], Guadalupe Mountains [National Park], Pine Spring Canyon, 1737 m. HT ♂, 28 August 1967, in USNM (type no. 68149).
carancahua, Marilopteryx   Noctuidae   33
    TL: Texas, Jackson Co., Deutschburg nr. Carancahua Creek. HT ♂, 6 March 1975, in USNM.
chihuahua, Tripudia   Noctuidae   45
    TL: Texas, Brewster Co., Big Bend National Park, Chihuahuan Desert nr. Nugent Mountain. HT ♂, 8 October 1969, in USNM.
chisosensis, Zale   Noctuidae   29
    TL: Texas, Jeff Davis Co., Davis Mountains, Mt. Locke, 2042 m. HT ♂, 10 June 1969, in USNM.
citeria, Hexorthodes   Noctuidae   57
    TL: Texas, Jeff Davis Co., Fort Davis. HT ♂, 11 June 1969, in USNM.
clarkei, Phaneta   Tortricidae   41
    TL: Texas, Hemphill Co., Canadian National Grassland, Lake Marvin. HT ♂, 9 October 1982, in USNM.
collilonga, Pelochrista   Tortricidae   44
    TL: Texas, Brown Co., Lake Brownwood State Park. HT ♂, 21 April 1966, in USNM.

coloradella, Rostrolaetilia   Pyralidae   **17**
TL: Colorado, [Pueblo Co.], Pueblo. HT ♀, July, in USNM (type no. 73284).
cottami, Oncocnemis   Noctuidae   **9**
TL: Texas, [Brewster Co.], Big Bend National Park, Basin, 1676 m. HT ♂, 10 May 1966, in USNM.
cruentana, Phaneta   Tortricidae   **30**
TL: Texas, Anderson Co., nr. Tennessee Colony, [Gus] Engeling Wildlife Management Area. HT ♂, 28 June 1978, in USNM (type no. 76733).
diabolana, Eucosma   Tortricidae   **26**
TL: Texas, Culberson Co., Sierra Diablo Wildlife Management Area, 1829 m. HT ♂, 31 March 1970, in USNM (type no. 75820).
dominicki, Carectocultus   Pyralidae   **16**
TL: Texas, Jackson Co., Deutschburg. HT ♂, 31 July 1972, in USNM (type no. 73242).
dorsonotata, Triozosneura   Pyralidae   **13**
TL: Texas, [Jeff Davis Co.], Davis Mountains, Mt. Locke, McDonald Observatory grounds. HT ♂, 27 August 1970, in USNM (type no. 72379).
dupla, Bertelia   Pyralidae   **20**
TL: Texas, Presidio Co., Shafter. HT ♂, 19 October 1973, in USNM (type no. 73530).
emendata, Hexorthodes   Noctuidae   **57**
TL: Texas, Jeff Davis Co., Fort Davis. HT ♂, 11 June 1969, in USNM.
eureka, Rostrolaetila   Pyralidae   **17**
TL: Utah, Eureka. HT ♂, 14 August 1911, in USNM (type no. 73285).
exculta, Paramiana   Noctuidae   **58**
TL: Texas, Jeff Davis Co., Mount Locke. HT ♂, 20 August 1984, in USNM.
fergusonella, Psorosina   Pyralidae   **39**
TL: Texas, Anderson Co., nr. Tennessee Colony, [Gus] Engeling Wildlife Management Area. HT ♂, 19 June 1982, in USNM.
franclemonti, Oxycnemis   Noctuidae   **4**
TL: Texas, [Brewster Co.], Big Bend National Park, Green Gulch, 1646 m. HT ♂, 3 April 1965, in USNM (type no. 68162).
fritillana, Eucosma   Tortricidae   **30**
TL: Texas, Anderson Co., nr. Tennessee Colony, [Gus] Engeling Wildlife Management Area. HT ♂, 28 June 1978, in USNM (type no. 76734).
furtiva, Ursia   Notodontidae   **8**
TL: [Texas, Brewster Co.], Big Bend National Park, Pine Canyon, 1585 m. HT ♂, 2 September 1964, in USNM (type no. 64648).
garneri, Drepanulatrix   Geometridae   **58**
TL: Texas, Uvalde Co., Garner State Park. HT ♂, 24 March 1985, in USNM.
gillaspyi, Copablepharon   Noctuidae   **19**
TL: Texas, Kleberg Co., Padre Island National Seashore. HT ♂, 28 September 1973, in USNM (type no. 73433).
graziella, Eucosma   Tortricidae   **4, 26**
TL: Texas, [Brewster Co.], Big Bend National Park, Green Gulch. HT ♂, 11 October 1966, in USNM (type no. 68164).
griselda, Eucosma   Tortricidae   **31**
TL: Texas, Brewster Co., Big Bend National Park, Chisos Basin. HT ♂, 7 April 1967, in USNM.
guttulana, Eucosma   Tortricidae   **26**
TL: Texas, Kleberg Co., Padre Island National Seashore. HT ♂, 19 July 1976, in USNM (type no. 75819).
habrolepis, Chlamydastis   Oecophoridae   **59**
TL: Texas, Cameron Co., Laguna Atascosa [National Wildlife Refuge]. HT ♂, 1 April 1978, in USNM.
hecate, Gloanna   Noctuidae   **37**
TL: Texas, Culberson Co., Sierra Diablo Wildlife Management Area. HT ♂, 11 June 1982, in USNM.

heppneri, Petrophila   Pyralidae   **35**
    TL: Texas, Kerr Co., [16.1 km] W of Hunt. HT ♂, 1 September 1980, in USNM.
heterogena, Oncocnemis   Noctuidae   **9**
    TL: Texas, [Brewster Co.], Big Bend National Park, Green Gulch. HT ♂, 27 August
    1965, in USNM (type no. 68148).
hieroglyphana, Grapholita   Tortricidae   **44**
    TL: Texas, [Culberson Co.], Guadalupe Mountains, Nickel Creek. HT ♂, 10 July 1968,
    in USNM.
insularis, Pimodes   Pyralidae   **21**
    TL: Texas, Kleberg Co., Padre Island National Seashore. HT ♂, 29 September 1975, in
    USNM (type no. 73652).
junctimacula, Aleptina   Noctuidae   **47**
    TL: Texas, [Brewster Co.], Big Bend National Park, Dugout Wells. HT ♂, 29 August
    1965, in USNM.
kendalli, Bucculatrix   Lyonetiidae   **49**
    TL: Texas, Bexar Co., Ebony Hill Research Station (Kendall residence). HT ♂, 19
    September 1984, in USNM.
kendalli, Zamagiria   Pyralidae   **6**
    TL: Texas, Jeff Davis Co., Fort Davis, Hospital Canyon, 1524 m. HT ♂, 11 July 1969,
    in USNM (type no. 71004).
kendallorum, Symmetrischema   Gelechiidae   **34**
    TL: Texas, Nueces Co., north Padre Island. HT ♂, 17 September 1981, in USNM.
lenticuligera, Glenoides   Geometridae   **12**
    TL: Texas, Hidalgo Co., Santa Ana National Wildlife Refuge. HT ♂, 15 February 1971,
    in USNM (type no. 72326).
linitipunctana, Phaneta   Tortricidae   **40**
    TL: Texas, Nueces Co., north Padre Island. HT ♂, 9 September 1974, in USNM.
longipectinaria, Hypomecis   Geometridae   **42**
    TL: Texas, Montgomery Co., Conroe. HT ♂, 30 April 1970, in USNM.
luctuosana, Epiblema   Tortricidae   (homonym—see *luctuosissima*)   **25, 53**
luctuosissima, Epiblema   Tortricidae   **25, 53**
    TL: Texas, Nueces Co., north Padre Island. HT ♂, 6 April 1978, in USNM (type no.
    75822).
margueritaria, Grotella   Noctuidae   **4**
    TL: Texas, [Brewster Co.], Big Bend National Park, Chihuahuan Desert nr. Nugent
    Mountain, 914 m.~HT ♂, 8 October 1966, in USNM (type no. 68163).
mayelisana, Phaneta   Tortricidae   **26**
    TL: Texas, Cottle Co., nr. Paducah, Matador Wildlife Management Area. HT ♂, 17
    April 1968, in USNM (type no. 75817).
mayelisaria, Glaucina   Geometridae   **3**
    TL: [Texas, Brewster Co.], Big Bend National Park, Government Spring. HT ♂, 29
    September 1965, in AMNH.
melusina, Neodavisia   Pyralidae   **46**
    TL: Texas, Starr Co., Roma. HT ♂, 4 April 1978, in USNM.
mendaciana, Suleima   Tortricidae   **41**
    TL: Texas, Brewster Co., Big Bend National Park, Dugout Wells. HT ♂, 28 September
    1981, in USNM.
mephisto, Neperigea [*Properigea*]   Noctuidae   **4**
    TL: Texas, Culberson Co., Sierra Diablo Wildlife Management Area, Sierra Diablo
    Mountains, NNW of Van Horn, 1676 m. HT ♂, 22–23 June 1965, in USNM (type no.
    68161).
minimella, Rostrolaetilia   Pyralidae   **17**
    TL: California, Inyo Co., Olancha. HT ♂, "June 24–30" in USNM (type no. 73281).
multistriatella, Ozamia   Pyralidae   **32**
    TL: Texas, Jeff Davis Co., Fort Davis. HT ♂, 25 March 1968, in USNM.

musetta, Phaneta   Tortricidae   **41**
    TL: New Mexico, Socorro Co., Gran Quivara National Monument, 2012 m. HT ♂, 1–3 July 1964, in USNM.
nymphana, Gretchena   Tortricidae   **41**
    TL: Texas, Anderson Co., nr. Tennessee Colony, Gus Engeling Wildlife Management Area. HT ♂, 15 April 1968, in USNM.
ovaliger, Atopothoures [=*Goya* Ragonot 1888]   Pyralidae   **15, 23**
    TL: Texas, [Kimble Co.], Junction. HT ♂, 21 August 1973, in USNM (type no. 73241).
padreella, Peoria   Pyralidae   **27**
    TL: Texas, Kleberg Co., Padre Island National Seashore. HT ♂, 24 June 1976, in USNM (type no. 76140).
paraplesiana, Sonia   Tortricidae   **25**
    TL: Texas, [Harris Co.], Houston. HT ♂, 5 June 1968, in USNM.
parvalbum, Homoeosoma   Pyralidae   **48**
    TL: Texas, Brewster Co., Big Bend National Park, Hot Springs. HT ♂, 4 April 1984, in USNM.
peorinella, Anderida   Pyralidae   **51**
    TL: Texas, Brewster Co., Big Bend National Park, K-Bar Research Station. HT ♂, 1 April 1984, in USNM.
pinalensis, Rostrolaetilia   Pyralidae   **17**
    TL: Arizona, [Gila Co.], Pinal Mountains, 1524 m. HT ♂, 15–30 April 1925, in USNM (type no. 73287).
placidissima, Rostrolaetilia   Pyralidae   **17**
    TL: Utah, Stockton. HT ♂, "IX.1.4", in USNM (type no. 73282).
salaciana, Eucosma   Tortricidae   **31**
    TL: Texas, Nueces Co., north Padre Island. HT ♂, 13 October 1979, in USNM.
salmocolor, Dasypyga   Pyralidae   **6**
    TL: Texas, Culberson Co., Sierra Diablo Wildlife Management Area, 1829 m. HT ♂, 1 September 1969, in USNM (type no. 71005).
septuosa, Tarachidia   Noctuidae   **58**
    TL: Texas, Cameron Co., Laguna Atascosa [National Wildlife Refuge]. HT ♂, 16 May 1974, in USNM.
serraticornis [*serraticorne*], *Copablepharon*   Noctuidae   **19**
    TL: Texas, Cottle Co., nr. Paducah, Matador Wildlife Management Area. HT ♂, 8 September 1966, in USNM (type no. 73432).
sierrae, Eucosma   Tortricidae   **41**
    TL: Texas, Culberson Co., Sierra Diablo Wildlife Management Area, 1951 m. HT ♂, 30 August 1970, in USNM.
signifera, Macrorrhinia   Pyralidae   **21**
    TL: Texas, Tyler Co., Town Bluff. HT ♂, 7 August 1975, in USNM (type no. 73651).
texanalis, Oenobotys   Pyralidae   **22**
    TL: Texas, Jeff Davis Co., Fort Davis. HT ♂, 5 October 1969, in CNC (type no. 13919); allotype-topotype ♀ in USNM.
texanella, Rostrolaetilia   Pyralidae   **17**
    TL: Texas, Jeff Davis Co., Davis Mountains, Mt. Locke. HT ♂, 4 July 1969, in USNM (type no. 73286).
texasana, Anopina   Tortricidae   **44**
    TL: Texas, Jeff Davis Co., [Davis Mountains], Mt. Locke, 2042 m. HT ♂, 26 April 1981, in USNM.
toddi, Oncocnemis   Noctuidae   **4**
    TL: Texas, [Brewster Co.], Big Bend National Park, Chihuahuan Desert nr. Dugout Wells, 914 m. HT ♂, 28 September 1965, in USNM (type no. 68165).
ustulatana, Eucosma   Tortricidae   **41**
    TL: Texas, Washington Co., Brenham. HT ♂, 4 June 1979, in USNM.
utahensis, Rostrolaetilia   Pyralidae   **17**
    TL: Utah, Richfield. HT ♀, 15 June 1930, in USNM (type no. 73283).

valliscola, Acronicta   Noctuidae   **4**
  TL: Texas, [Brewster Co.], Big Bend National Park, Green Gulch, 1585 m. HT ♂, 10
  May 1966, in USNM (type no. 68159).
verecundana, Phaneta   Tortricidae   **26**
  TL: Texas, Hemphill Co., Gene Howe Wildlife Management Area nr. Canadian. HT
  ♂, 15 August 1971, in USNM (type no. 75818).
viridivallis, Glyphocystis   Pyralidae   **13**
  TL: Texas, [Brewster Co.], Big Bend National Park, Green Gulch. HT ♂, 28 March
  1971, in USNM (type no. 72380).

RARE AND INTERESTING LEPIDOPTERA

Species are arranged alphabetically and keyed to the bibliography.

addens, Eulepidotis   Noctuidae   (first TX & US, ♀ fig.)   **56**
admixta, Quasisalebria   Pyralidae   (first TX)   **6**
alatella, Myelopsis   Pyralidae   (first TX)   **6**
albiplagiatella occidentalis, Pima   Pyralidae   (first TX)   **6**
aleptivoides, Aleptina   Noctuidae   (new comb., ♂, ♂ & ♀ genit. fig.)   **47**
alpinata, Eupithecia   Geometridae   (♂ & genit. fig.)   **52**
anartoides, Radara [Matiloxis]   Noctuidae   (first TX & US (?), ♂ fig.)   **11**
angustalatella, Ethmia   Oecophoridae   (first TX & US, ♂, ♀ & genit. fig.)   **54**
ardiferella, Rostrolaetilia   Pyralidae   (HT ♀, ♂ & ♀ genit. fig.)   **17**
arizonensis, Daulia   Pyralidae   (♂ fig.)   **56**
atalanta, Scordylia [Heterosia]   Geometridae   (first TX & US (?), ♀ fig.)   **11**
auranticella(=rossi, corrected in #14), Dioryctria   Pyralidae   (first TX)   **6**
australella, Zamagiria   Pyralidae   (TX TL conf.)   **6**
baracoalis, Lamprosema   Pyralidae   (♀ fig.)   **56**
basipunctaria, Sigela   Noctuidae   (first TX (?), ♂ fig.)   **11**
belfragei, Heterocampa   Notodontidae   (comp. with *H. benitensis*)   **7**
bolteri, Eupithecia   Geometridae   (♂ & genit. fig.)   **52**
brillians, Miracavira   Noctuidae   (♂ fig.)   **56**
cana, Sparganothis   Tortricidae   (♂ fig.)   **56**
clinopetes, Aleptina   Noctuidae   (new comb., ♂, ♂ & ♀ genit. fig.)   **47**
cocoata, Eupithecia   Geometridae   (first TX)   **52**
coloradensis, Eupithecia   Geometridae   (first TX)   **52**
collaris, Nystalea   Notodontidae   (larval foodplant, ♀ fig.)   **56**
concors, Glympis   Noctuidae   (TX records, ♂ fig.)   **11**
condigna, Anadelosemia   Pyralidae   (first TX)   **6**
consimilis, Evergestis   Pyralidae   (TX records, ♂ fig.)   **11**
costata, Stemhorrhages   Pyralidae   (♂ fig.)   **56**
cucullidea, Emariannia   Noctuidae   (TX records, ♂ fig.)   **11**
daemonalis, Iscadia   Noctuidae   (TX records, ♂ fig.)   **11**
dissimulatrix, Actrix   Pyralidae   (first TX)   **6**
donysa, Amplypterus   Sphingidae   (first TX & US, ♀ fig.) [=*Adhermarius blanchar-*
  dorum Hodges 1985]   **11**
eburneata, Scopula   Geometridae   (♂ fig.)   **56**
edentatus, Stiriodes   Noctuidae   (first TX, ♂ fig.)   **43**
edna, Eupithecia   Geometridae   (♂ & genit.)   **52**
electrica, Goniocarsia   Noctuidae   (♀ fig.)   **56**
erronella, Unadilla   Pyralidae   (first TX & US)   **6**
eudoreella, Diviana   Pyralidae   (♂ fig.)   **56**
formularis, Lesmone   Noctuidae   **56**
fredericki, Eupithecia   Geometridae   (OD, ♂ & genit. fig.—Knudson)   **52**
fufius, Lesmone   Noctuidae   (♂ fig.)   **56**
funeralis, Acronicta   Noctuidae   (first TX, ♂ fig.)   **56**
grandis [grande], Copablepharon   Noctuidae   (TX records)   **19**

INTENSIVELY WORKED COLLECTING LOCALITIES

Although some collections were made in other states (Colorado and New Mexico), Texas was of primary interest and intensively worked by Blanchard. In early 1962 he began preparing a card index of species found in Texas. Taxonomic arrangement was primarily that of McDunnough's 1938 and 1939 Check Lists. For each of more than 3000 species he cited the original description, other significant taxonomic references, and listed specific records including his own captures. The card file was designed for his personal use and as a memory jogger. Locality data rarely included details.

Because these localities apply to approximately 100,000 specimens in various museums and private collections, and because future workers will be interested in specific localities for spatial distribution and life history studies, more complete locality data are provided here. During one of our last visits André permitted me to make photocopies of his "Lepidoptera Card File" for my own data-bank. It was his wish, however, that the file eventually go to Edward C. Knudson, coauthor of about half of his published papers. It did. Collections were made in more than 57 counties; there are 254 in the State, thus the sample size was 22% or more of the total.

Locations are arranged alphabetically, and each includes Texas county and other details.

Addicks.   Harris Co., W of Houston off IH-10.

Aguja Canyon.   Jeff Davis Co., Davis Mountains, Tx Ranch road 1832, 18 km W of Tx Hwy 17 at Boy Scout Camp.

Alpine.   Brewster Co., within city of Alpine or nearby.

Alpine Girl Scout Camp.   Jeff Davis Co., off Tx Hwy 118, 23 km NNW of Alpine nr. Miter Peak.

Aransas National Wildlife Refuge.   Aransas Co., 11 km S of Austwell (133,982+ ha).

Artesia Wells.   Dimmit-LaSalle counties, Chaparral Wildlife Management Area, N of Farm Road 183, 8 km W of Artesia Wells. (Collections mostly in LaSalle Co.)

Balmorhea State Park.   Reeves Co., Tx Hwy 17 nr. Toyahavale.

Bastrop State Park.   Bastrop Co., Tx Hwy 21 nr. Bastrop.

Bear Canyon.   (See Guadalupe Mountains National Park.)

Bear Creek.   Harris Co., Bear Creek Park, recreation area in NW Houston.

Belton Reservoir.   Bell Co., Lake Belton nr. Belton.

Big Bend National Park.   Brewster Co. (1,746,997 ha)
   Basin

Chihuahuan Desert nr. Nugent Mountain (Nugent Mt. draw)
Chisos Mountains (principal mts. within Park)
Croton Spring
Dugout Wells
Government Spring
Grapevine Hills & Spring
Green Gulch
K-Bar Research Station (old ranch house nr. Hq.)
Oak Spring
Old Ranch (Burro Messa, road to Castilon)
Panther Canyon (draw, spring) below Park Hq.
Panther Junction
Pine Canyon
Rio Grande Village
San Vicente Crossing
   (All locations indicated on maps available at Park Hq.)
Black Gap.   Brewster Co., Black Gap Wildlife Management Area, Ranch road 2627, 56 km SE of Marathon (254,513+ ha).
Blanco State Park (or only Blanco).   Blanco Co., on Blanco River at Blanco city.
Brazos River.   (See Spivey Crossing.)
Caddo Lake State Park (or only Caddo Lake).   Harrison Co., nr. Kanak.
Camp Strake.   (See Conroe.)
Canadian.   (See Gene Howe Wildlife Management Area.)
Chihuahuan Desert nr. Nugent Mt.   (See Big Bend National Park.)
Churchill Bridge.   Brazoria Co., SW of Brazoria off Tx Hwy 36 at San Bernard River.
Clebourne State Park (or only Cleburne).   Johnson Co., SW of Clebourne off US Hwy 67.
Coldspring.   San Jacinto Co., Sam Houston National Forest, Tx Hwy 2025, 5 km S of Coldspring, Double Lake recreation area.
College Station.   Brazos Co., joins city of Bryan.
Conroe.   Montgomery Co., Camp Strake, private recreation area at Conroe.
Cypress & Cypress Lake.   Harris Co., NW of Houston, US Hwy 290/Tx Hwy 6.
Dam B (now Steinhagen Lake).   Tyler Co., 29 km E of Woodville on Neches River. (Traps were usually set near the spillway or along W bank of reservoir.)
Deussen Park.   Harris Co., Alexander Deussen Park, Houston (N Lake Houston Parkway on Lake Houston).
Deutschburg.   Jackson Co., a community nr. Carancahua Creek S of Francitas.
Dewalt.   Fort Bend Co., small community on Tx Hwy 6.
Don George Lake.   Fort Bend Co., 16 km SE of Richmond.
Eagle Lake.   Colorado Co., US Hwy 90-A.
Eagle Pass.   Maverick Co., private property nr. Eagle Pass.
El Rancho Cima.   Comal/Hays counties, Tx Hwy 32, 24 km W of San Marcos, Boy Scout Camp. (Most collections were made in Hays Co.)
Falcon Heights.   Zapata Co., nr. Falcon Reservoir on Rio Grande.
Falcon State Park.   Zapata Co., off US Hwy 83 on Falcon Reservoir.
Frijoles.   (See Guadalupe Mountains National Park.)
Garner State Park (or only Garner).   Uvalde Co., off US Hwy 83 40 km N of Uvalde.
Gene Howe Wildlife Management Area.   Hemphill Co., FM road 2266, 10 km E of Canadian (14,383+ ha).
George West.   Live Oak Co., private property nr. George West.
Goodrich.   Polk Co., S of Livingston. (Collection in Sam Houston National Forest.)
Gray Ranch.   (See Jeff Davis Co.)
Guadalupe Mountains National Park.   Culberson & Hudspeth counties off US Hwy 62/ 180 (191,546+ ha). (All collections made in Culberson Co.)
Bear Canyon
Frijoles, nr. Manzanita Spring
McKittrick Canyon

Pine Spring Canyon (or only Pine Canyon)
Smith Canyon
    (Local National Park map shows all locations.)
Guadalupe River.   Comal Co., on Guadalupe River NNW of New Braunfels, private
    recreation camp nr. 4th crossing of river.
Gus Engeling Wildlife Management Area.   Anderson Co., US Hwy 287, 32 km NW of
    Palestine nr. Tennessee Colony (26,392+ ha).
Harlingen.   Cameron Co., private property nr. Harlingen.
Hempstead.   Waller Co., US Hwy 290/Tx Hwy 6.
Huntsville State Park (or only Huntsville).   Walker Co., off Tx Hwy 19, 8 km S of
    Huntsville.
Houston.   Harris Co., unless otherwise indicated, 3025 Underwood Street, Blanchard's
    residence.
Indian Village.   Polk Co., Alabama & Coushatta Indian Reservation, off US Hwy 190,
    24 km E of Livingston.
Jeff Davis Co.
    Fort Davis
    Hospital Canyon, behind Old Fort Davis Historic Site
    Limpia Canyon, Tx Hwys 17 & 118 nr. Fort Davis
    Mt. Livermore, off Tx Hwy 166, 8 & 13 km SE of, on Friend's Ranch (private)
    Tom R. Gray Ranch, Tx Hwy 166 WSW of Fort Davis (private)
    W. B. Sharp Ranch, Tx Hwy 17 NNE of Fort Davis (private)
Junction.   Kimble Co., V. H. Ranch, US Hwy 377, 14 km SW of Junction on South Llano
    River.
Kerrville State Park (or only Kerrville).   Kerr Co., on Guadalupe River at Kerrville.
Kerr Wildlife Management Area.   Kerr Co., Tx Ranch road 1340, 45 km W of Kerrville
    (16,044+ ha).
Laguna Atascosa. (See Laguna Atascosa National Wildlife Refuge.)
Laguna Atascosa National Wildlife Refuge.   Cameron/Willacy counties on Laguna Madre
    (111,558+ ha). (All collections made in Cameron Co.)
Laguna Park.   Hill Co., small town, collections on grounds of local motel.
Lake Brownwood State Park.   Brown Co., off Tx Hwy 279, 26 km NNW of Brownwood.
Lake Corpus Christi State Park.   San Patricio Co., off Tx Hwy 359, 6 km SW of Mathis.
Lake o' the Pines.   Marion Co., private recreation area, N side of lake.
Lake Travis.   Travis Co., recreation area on Lake Travis nr. Bee Cave off Tx Hwy 71.
Lake Walk.   Val Verde Co. Before 1969 this and Devils Lake were flood control reservoirs
    on the Devils River 11 and 16 km above the Rio Grande. Following completion of
    Amistad Dam and Reservoir on the Rio Grande, both Lake Walk and Devils Lake
    ceased to exist, having been inundated by water from Amistad.
Livingston.   Polk Co.
Matador Wildlife Management Area.   Cottle Co., W of US Hwy 83, 18 km NW of
    Paducah (69,242+ ha).
Mathis.   San Patricio Co., private property nr. Mathis.
McKittrick Canyon.   (See Guadalupe Mountains National Park.)
Memorial Park.   Harris Co., Houston city park.
Morgan's Point.   Harris Co., E of Pasadena on San Jacinto Bay.
Mount Locke.   Jeff Davis Co., Davis Mountains, off Tx Hwy 118, 26 km NW of Fort
    Davis, grounds of McDonald Observatory.
New Waverly.   Walker Co., Sam Houston National Forest, Stubblefield recreation area
    W of New Waverly.
Nickel Creek.   Culberson Co., US Hwy 62/180, a small community 8 km NE of Pine
    Springs. (Collections made in Guadalupe Mountains National Park.)
Padre Island (Tx offshore island spanning 5 counties).
    North Padre Island. Nueces Co.
    Padre Island National Seashore. Kleberg and Kenedy counties. (Collections made in
    Kleberg Co.)

South Padre Island. Willacy Co. (north) and Cameron Co. (south). (Collections made in Cameron Co.)

Paducah.   (See Matador Wildlife Management Area.)

Palo Duro Canyon State Park.   Randall Co., Tx Hwy 217, 19 km E of Canyon.

Pedernales Falls State Park.   Blanco Co., Tx Farm road 2766, 13 km E of Johnson City on Pedernales River.

Point Comfort.   Jackson Co., private property on Lavaca Bay.

Port Alto.   Calhoun Co., W shore Carancahua Bay. Blanchard had a beach house here destroyed by Hurricane Celia 3 August 1970.

Port Lavaca.   Calhoun Co., on Lavaca Bay.

Possum Kingdom.   Palo Pinto Co., Possum Kingdom State Park, on W shore of Possum Kingdom Reservoir.

Raymondville.   Willacy Co., private property nr. Raymondville.

Richmond.   Fort Bend Co., private property, E bank of Brazos River off US Hwy 59.

Rio Frio.   Real Co., small village on Frio River off US Hwy 83, 13 km S of Leakey.

Rosenberg.   Fort Bend Co., nr. Rosenberg (private).

Ruidosa-Hot Spring.   Presidio Co., 10 km ENE of Ruidosa on Hot Springs Creek, private recreation area.

Sabinal.   Uvalde Co., private recreation area nr. Sabinal.

San Antonio.   Bexar Co., Mountain View Acres, 5598 Mt. McKinley Drive NE (R. O. & C. A. Kendall residence which they dubbed Ebony Hill Research Station, "EHRS").

San Benito.   Cameron Co., private property nr. San Benito.

Santa Ana Refuge (or Santa Ana).   Hidalgo Co., Santa Ana National Wildlife Refuge, off US Hwy 281 S of Alamo (4885+ ha).

Santa Rosa.   Cameron Co., Las Palomas Wildlife Management Area—Longoria Tract, Tx Farm road 506, 6 km N of Santa Rosa.

Sealy.   Austin Co., US Hwy 90 at Brazos River (private).

Shafter.   Presidio Co., private property, recreation area.

Sharp Ranch.   (See Jeff Davis Co.)

Sheffield.   Pecos Co., Tx Hwy 349 at US Hwy 290 nr. Pecos River.

Sheldon.   Harris Co., Sheldon Wildlife Management Area, US Hwy 90, 16 km E of Houston (6046+ ha).

Shepherd.   San Jacinto Co., small community on US Hwy 59. (Collections in Sam Houston National Forest.)

Sierra Diablo.   Culberson Co., Sierra Diablo Wildlife Management Area, 51 km NW of Van Horn (19,251+ ha).

Smith Point.   Chambers Co., small community on E shore of Trinity Bay.

Spivey Crossing.   Hill Co., 11 km SE of Laguna Park, Tx Farm road 2114 at Brazos River, J. W. Glenn Ranch.

Spring.   Harris Co., small town on US Hwy 75 N of Houston (private property).

Tennessee Colony.   Collections made at Gus Engeling Wildlife Management Area.

Town Bluff.   Tyler Co., small village adjacent to Steinhagen Lake dam (formerly Dam B), Tx Farm road 92.

Utopia.   Uvalde Co., Tx Hwy 187, NE corner of county, 2 km S of Utopia, Old Waresville River Resort.

Van Horn.   Culberson Co., private property near Van Horn.

Voshell.   Cameron Co., Las Palomas Wildlife Management Area—Voshell Tract, Tx Farm road 511, 4 km SE of Brownsville.

Warren.   Tyler Co., US Hwy 69/287, small town.

Welder Wildlife Foundation Refuge.   San Patricio Co., US Hwy 77, 13 km NE of Sinton (19,768 ha).

Westfield.   Harris Co., small community off IH-45 N of Houston.

Zapata.   Zapata Co., private property nr. town.

ACKNOWLEDGMENTS

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BOOK REVIEWS

A REVISION OF THE GENUS *HYPOCHRYSOPS* C. & R. FELDER (LEPIDOPTERA: LYCAENIDAE). D. P. A. Sands. 1986. Entomonograph vol. 7. E. J. Brill/Scandinavian Science Press, Leiden. 116 pp., 2 color plates. About $38.25.

Sands's revision of the primarily Australian Region hairstreak genus *Hypochrysops* (Lycaenidae) is excellent. First and foremost, Sands knows these butterflies intimately. He has studied them in the field and museum, and clearly communicates his encyclopedic knowledge of them. There are 57 species—including 4 new ones—that can now be identified using the wing pattern keys to males and females. Almost half of the species are illustrated on two superb color plates. Sands figures male genitalia for each species, and comments on identification, larval foodplants, myrmecophily, and distribution. This information will be of interest to all students of Australian Region butterflies.

Sands's classification differs from that in previous books, such as D'Abrera (1977, Butterflies of the Australian Region, Lansdowne, Melbourne) because *Hypochrysops* had been confused with *Waigeum*. *Hypochrysops* species have red bands bordered with silver-green metallic markings while *Waigeum* resemble the distinctive "*Danis* wing pattern" shared by a variety of unrelated Australian Region blues and hairstreaks (Eliot, J. N. 1973. Bull. Brit. Mus. [Nat. Hist.] 28:399). Sands synonymizes these two genera because they do not differ structurally and because there are transitional forms. As this brief description indicates, *Hypochrysops* are beautiful butterflies.

Two scientific highlights are noteworthy. First, Sands quantifies some of the variation that he finds in wing patterns and legs. The use of means and standard errors allows objective assessment of previous taxonomic results based on wing pattern and leg variation; hopefully Sands's example will be followed by others. Second, Sands notes that "parts of the genitalia are almost membranous when specimens are freshly emerged and do not develop complete sclerotisation until about three days after emergence." If this observation, which I believe to be original, is widely true, it would account for some genital variation found in butterflies.

Sands admirably discusses the systematic position of *Hypochrysops* among the hairstreaks. He presents an identification key to the four genera of the relatively homogeneous *Hypochrysops* Section. Clench (1955, Ann. Carnegie Mus. 33:261–274) considered these butterflies to be close relatives of the New World eumaeine hairstreaks, but Eliot (above) placed them in the tribe Luciini. Sands accepts Eliot's classification, but I do not believe there is enough published information to resolve these differing views, one of the very few points on which I disagree with Sands.

Despite my high praise, there are a few minor weaknesses with the book. Sands does not illustrate the female genitalia, an unnecessary omission. His classification is based mostly on overall similarity, not phylogeny, and I hope that he will consider a phylogenetic analysis as his next project. Along the same lines, he presents a diagnosis of *Hypochrysops*, but does not specify derived character states that "define" the genus. The biggest drawback, however, is the $38.25 price tag for a slim 116 page book with two color plates. Apparently, it was priced for libraries, not individuals. However, those interested in the Lepidoptera of the Australian Region cannot afford not to have this excellent work.

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NOCTUELLES ET GÉOMÈTRES D'EUROPE. DEUXIÈME PARTIE. GÉOMÈTRES. VOLUME III—
1917–1919. Jules Culot. Reprint edition, 1987. Apollo Books, Svendborg, Denmark. Order
from: Apollo Books, Lundbyvej 36, DK-5700 Svendborg, Denmark. Vols. III–IV, DKK
1380.00.

This is an exact copy of the original volume, with 269 pp. and 37 color plates (figs. 1–
771)—it is so identical, in fact, that the listings on the page of errata were not entered
in the text of the reprint. The reprint edition is handsomely done, using glossy paper
(which the original did not have) for both the text and plates; the latter are grouped
together at the back instead of being randomly distributed throughout the text (as in the
original). The figures were made from paintings and are all in color, always showing just
half the moth, even though there is more than enough room to portray the entire insect;
there has been a small loss of clarity and detail, and the colors do not always come up
to the standards of the original, but the differences are usually small.

This volume amounts to a descriptive and illustrated edition of Staudinger and Rebel
(1901, *Catalog der Lepidopteren des Palaearctischen Faunengebietes*) as it pertains to
Europe. The present volume does not have any descriptions or even indications of any
higher categories, much less keys to separate them; the only descriptive material is on
the specific level and below. No bibliographies or synonymies are given; you have to refer
to Staudinger and Rebel for references to original descriptions and other literature.

The Geometridae are covered in volumes 3 and 4 of this series. The family is arbitrarily
chopped in half so that the two volumes will be approximately the same size. While this
may make sense from a publisher's point of view, it doesn't from a systematic one. Volume
3 includes what today we call the Oenochrominae, Geometrinae, and part of the La-
rentiinae (up to but not including *Eupithecia*). The Archiearinae is not included because
Staudinger and Rebel placed *Archieris* Hübner (*Brephos* auct.) as a separate family, the
Brephidae.

Unless you are fairly well acquainted with the European geometrids, this book poses
a number of problems, beginning with the lack of definitions of the higher categories.
Without generic descriptions or diagnoses it may be difficult to properly place a given
species, as some members of this family look disconcertingly similar but may belong to
entirely different genera. If you are satisfied with the "picture book approach" you may
be satisfied with Culot—but you take your chances on the identifications.

Because the scientific names date from 1901, and no new scientific research has been
included since then, this book may be of more interest to the antiquarian than to today's
collectors. I find a book published just before Culot's to be much more useful; this is L.
B. Prout's *Palearctic Geometridae* (*in* A. Seitz, 1912–16 [English edition], *The Macro-
lepidoptera of the World*, Vol. 4). Prout's encyclopedic knowledge of the geometrids
enabled him to do a better job of classification, and all the higher categories are defined.
A modern treatment is given by W. Forster and T. A. Wohlfahrt in their *Die Schmet-
terlinge Mitteleuropas*; these authors do not hesitate to illustrate venation, antennae, and
the genitalia of both sexes whenever needed, as well as colored plates of the adults.

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A History of the Hope Entomological Collections in the University Museum Oxford with Lists of Archives and Collections. Audrey Z. Smith. 1986. Clarendon Press, Oxford. 172 pp.

This short but informative book is divided into two parts. The first seven chapters tell the story of Rev. Frederick William Hope, his collections, and his quest to insure that they would be preserved, protected, and studied. The second and more significant part of the book contains five appendices. These list many of the holdings of the Hope Collections' archives as well as names of individual donors and the collections they gave. Included in other appendices are a transcript of Rev. Hope's Deed of Gift and an Oxford committee's reaction to the Deed.

The author of this book is the Hope Librarian. Her attempt in the first third of the book to tell the history of Hope and his collections works fairly well. The text follows a logical sequence discussing Rev. Hope, curators of his collections, the collections themselves, the Hope Professors, and a list of scholars associated with the Collections. Unfortunately, little detail is provided in the chapter examining Rev. Hope's life. As a wealthy gentleman-collector of the 19th century, his story may not differ from some others, but one cannot help wondering what his particular areas of interest were, and whether he made any lasting contributions to science through his activities.

The other chapters also might have benefitted from additional detail, but they are sufficient to give the reader an idea of the importance of the Hope Collections. The chapter on the library of the Collections probably belongs in an appendix where other information regarding specific holdings has been placed.

The major contribution of this book may be found in its first two appendices. For researchers interested in studying particular entomologists, Appendix A will be invaluable. Consisting of an alphabetical list of archival holdings, the list is not complete, but one glance at it indicates the vast quantity and quality of material in the Archives. Following each name in the appendix is a brief description of the material held. Holdings include correspondence, diaries, field notes, plates, paintings, and other media of entomologists from the late 18th to the late 20th centuries. Appendix B is an alphabetical list of donors with a description of the donation. It should be particularly valuable when used with Appendix A. Lepidopterists are common in both appendices.

Lepidopterists will find *A History of the Hope Entomological Collections* to be a useful tool for research. Many archival repositories and museums contain priceless materials that go unused because researchers are unaware of their existence. A publication such as this does researchers a true service by informing them of the holdings of a major facility. This is not a book that lepidopterists should be anxious to acquire for their personal libraries. It is, however, a generally well crafted work that all science libraries should own.

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(New names in **boldface**)

NOTICE TO CONTRIBUTORS

Contributions to the *Journal* may deal with any aspect of the collection and study of Lepidoptera. Categories are Articles, General Notes, Technical Comments, Book Reviews, and Obituaries. Short manuscripts concerning new state records, current events, and notices should be sent to the *News*, June Preston, Editor, 832 Sunset Drive, Lawrence, Kansas 66044 U.S.A. *Journal* contributors should prepare manuscripts according to the following instructions.

Abstract: An informative abstract should precede the text of Articles.

Key Words: Up to five key words or terms not in the title should accompany Articles, General Notes, and Technical Comments.

Text: Manuscripts should be submitted in *triplicate*, and must be typewritten, *entirely double-spaced*, with wide margins, on one side only of white, letter-sized paper. Titles should be explicit, descriptive, and as short as possible. The first mention of a plant or animal in the text should include the *full scientific name* with *author*, and *family*. Measurements should be given in metric units; times in terms of the 24-hour clock (0930 h, not 9:30 AM). Underline only where *italics* are intended.

Literature Cited: References in the text of Articles should be given as Sheppard (1959) or (Sheppard 1959, 1961a, 1961b) and listed alphabetically under the heading LITERATURE CITED, in the following format without underlining:

SHEPPARD, P. M. 1959. Natural selection and heredity. 2nd ed. Hutchinson, London. 209 pp.
————— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10:165–216.

In General Notes and Technical Comments, references should be shortened and given entirely in the text as P. M. Sheppard (1961, Adv. Genet. 10:165–216) or (Sheppard, P. M., 1961, Sym. R. Entomol. Soc. London 1:23–30) without underlining.

Illustrations: Only half of symmetrical objects such as adults with wings spread should be illustrated, unless whole illustration is crucial. Photographs and drawings should be mounted on stiff, *white* backing, arranged in the desired format, allowing (with particular regard to lettering) for reduction to fit a *Journal* page. Illustrations larger than letter-size are not acceptable and should be reduced photographically to that size or smaller. The author's name and figure numbers as cited in the text should be printed *on the back* of each illustration. Figures, both line drawings and photographs, should be numbered consecutively in Arabic numerals; "plate" should not be employed. Figure legends must be typewritten, double-spaced, *on a separate sheet* (not attached to illustrations), headed EXPLANATION OF FIGURES, with a separate paragraph devoted to each page of illustrations.

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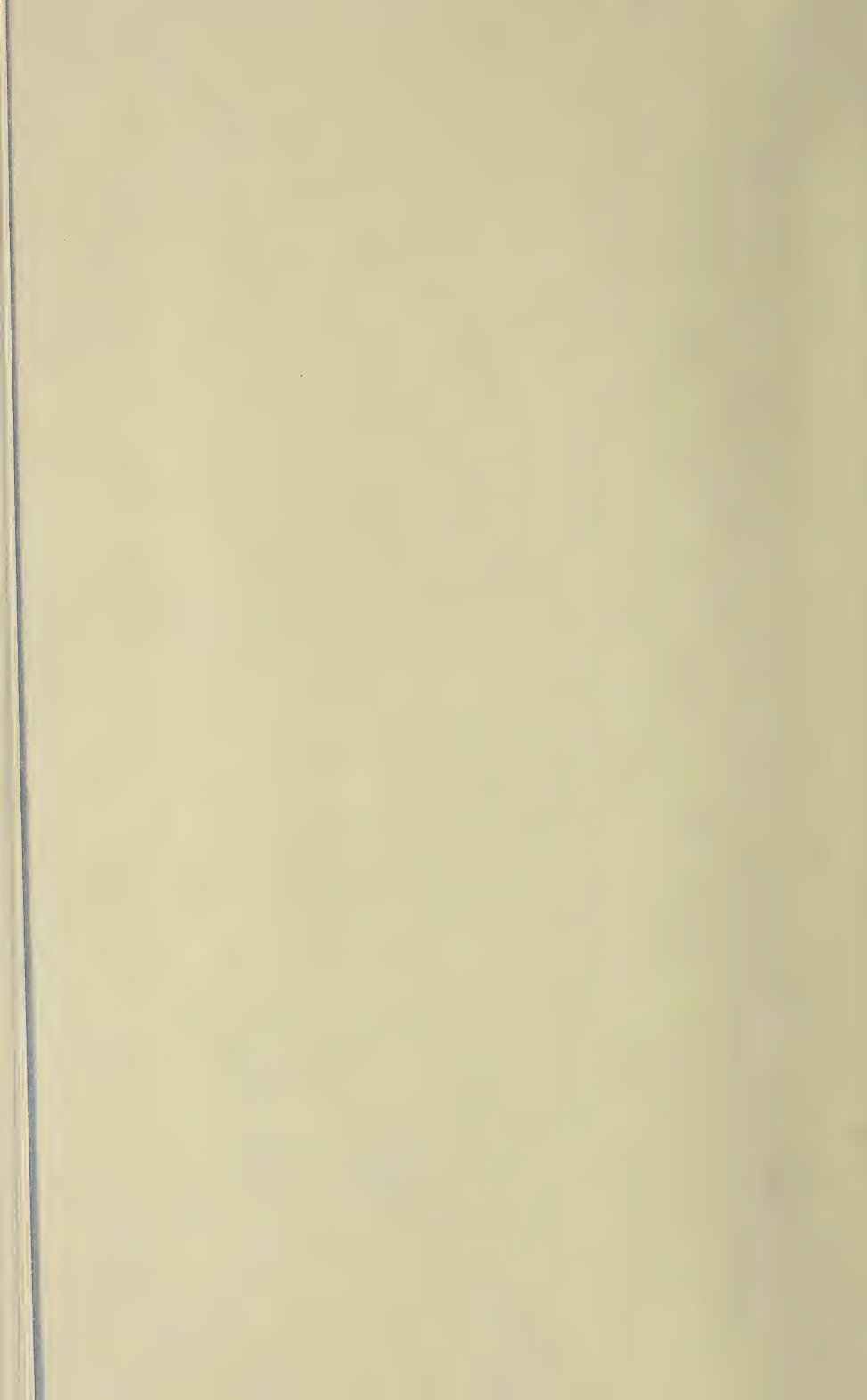
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